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STUDIES ON THE LIFE HISTORIES OF VARIOUS SPECIES OF ARTHROPLEONE COLLEMBOLA

By S. Milne

(*West of Scotland Agricultural College, Glasgow*)

[Communicated by Dr. J. W. H. Lawson]

Introduction

The life cycles of only a few species of Collembola have so far been investigated and no information has hitherto been available on the life histories of the species encountered during the field studies on the fauna under bracken reported by the present author (Milne, 1959). The species on which observations were made and reported here are *Tullbergia krausbaueri* (Boerner), *Onychiurus furcifer* Boerner, *O. latus* Gisin, *O. procampatus* Gisin, *Folsomia candida* Willem, *Isotoma viridis* Bourlet and *Neanura muscorum* (Templeton).

Technique

The primary requirement in the rearing of most soil arthropods under laboratory conditions is the maintenance of a high relative humidity in the culture vessel. This has been achieved in various ways by previous workers on Collembola. Ripper (1930) and Strebel (1932) used a substrate of soil, which, although giving a closer approach to natural conditions, renders continuous observation difficult. Moistened filter paper has been widely used, in small containers and tubes, to ensure high humidity level in studies on arthropods, and was used by Britt (1951) in his study of *Hypogastrura armata* Nicolet. The introduction by Searls (1928) of a technique for rearing Symphylids using plaster of Paris as a moisture source helped also to solve the problem of providing a suitable stable substrate for the animals. In a recent study of arthropleone Collembola, Schaller (1953) used a plaster of Paris block with glass-covered observation cells. The addition of powdered charcoal before mixing the plaster assists the observation of unpigmented animals (Wharton, 1946 ; Edwards, 1955). Petri dishes 7 cm. in diameter, with a layer of plaster 2–3 mm. in depth, were used as breeding dishes in the present study. To observe the development of *Folsomia candida*, cultures were made in small Petri dishes 4 cm. in diameter, similarly treated with plaster. Plaster blocks, with cells for individual insects, as described by Edwards (1955), were used for observing other species. Water was added to these dishes every week, a few drops only being required. Cultures were attempted in temperature controlled conditions at 5° C. ± 2°, 12° C. ± 1°, and 24° C. ± 1°.

Food was provided in the form of bracken spores, which were found to be suitable for most species. This material has advantages over yeast, starch and other matter previously used as food for Collembola in culture—the spores are easily applied and evenly spread over the culture medium ; there is little deterioration of the food, and fungal contaminants are not encouraged. These properties make frequent changes of the food material unnecessary.

Contamination of the eggs in the early stages of development by fungi, mainly *Penicillium* sp., caused difficulty. The growth of mycelia on the egg surface caused shrivelling and the death of most of the affected eggs. This difficulty was overcome, to some extent, by sterilising the culture dishes before use and by brushing the eggs periodically with distilled water. Fungi pathogenic to eggs of Collembola have been previously reported by Goto (1956).

Measurements were made, using reflected light, by means of a micrometer eyepiece. Owing to the difficulty of maintaining continuous direct observation of individuals of *F. candida*, measurement of growth in this species was made by removing ten individuals at intervals from a mass culture, in the small Petri dishes, from eggs laid within 24 hours. Development of the other species was observed from specimens in individual plaster block cells 8–10 mm. in diameter and 5 mm. in depth. A considerable number of individuals were reared, without accurate measurement, for the study of maturation, number of eggs and other aspects of their biology. One outstanding difficulty in making a precise study of these species is the lack of conspicuous sexual dimorphism, so that the sexes could not be determined with any accuracy in life. A 1 : 1 sex ratio has been assumed but this must be regarded with caution as there have been reports of a predominance of females in populations of certain species (Ripper, 1930).

Specimens were obtained from soil and humus under bracken (*Pteridium aquilinum* (L.) Kuhn) at Drumclog Moor, Milngavie, Dunbartonshire, by extraction on Berlese funnels. The insects were collected in a vessel containing water, from the surface of which they were removed to breeding dishes.

Results

Tullbergia krausbaueri Boerner

This is a small unpigmented species with a maximum length of less than 1 mm. It has been found mainly in the deeper layers of the soil and is widely distributed. Eyes and furca are absent and movement is rather sluggish. The eggs are smooth, unpigmented and globular and are indistinguishable, except by their size, from the eggs of those species of *Onychiurus* which were investigated. Before development the eggs measure 0·09–0·10 mm. in diameter and are laid either singly or in pairs on the surface of the culture medium. Developing eggs become flattened and disc-like in shape, measuring 0·13 mm. in diameter immediately before hatching. Hatching takes place by splitting of the chorion across the width of the disc. Newly hatched individuals are similar to the adults in appearance, except in lack of opacity, and measure 0·24 mm. in length. Development of the eggs took from 15 to 20 days at 12° C. No development occurred at 5° C. or 24° C. Sexual maturity was attained from 30 to 40 days after hatching, in the third instar, at 12° C. The growth of 15 individuals at this temperature is shown on Table I. Ecdyses occurred at intervals

Table I.—*Post-embryonic development of* Tullbergia krausbaueri *at 12° C. from observation of* 15 *individuals*

	Instar			
	1	2	3	4
Length (mm.)	0·24–0·39	0·39–0·45	0·45–0·54	0·54–0·63
Time for development in days (mean) .	8	20·1	28·1	43·9
Standard deviation	1·51	3·04	3·58	3·33

of 8–15 days, and continued throughout life at irregular intervals, without appreciable change in length after that of 0·63 mm. had been attained. Eggs were laid at 5° C., 12°C., and 24°C. assuming a sex ratio of 1 : 1, a mean of 10 eggs was laid by each female at 12° C. At 12° C. in the laboratory adults survived for more than six months.

Onychiurus furcifer Boerner

O. furcifer is an unpigmented species with no eyes, and a distinct but small furca, which distinguishes it from species of the family Onychiuridae. The eggs measure 0·17–0·19 mm. in diameter before development. Development appears to be similar

to that of *Tullbergia krausbaueri*, the diameter of the egg increasing to 0·21 mm. before hatching. Groups of up to six eggs were laid on the surface of the culture medium or in cavities with a small opening to the surface. Development of the egg took 26–30 days at 12° C. and 11–15 days at 24° C. Newly hatched specimens measured 0·42 mm. in length and 0·12 mm. in head width. The subsequent growth of 15 specimens in plaster block cells was observered and measurements made at intervals (Table II). Four ecdyses at intervals of two to four weeks were observed and sexual

TABLE II.—*Post-embryonic development of* Onychiurus *spp. at* 12° *C. based on observation of* 10 *individuals of* O. latus *and* 15 *individuals each of* O. procampatus *and* O. furcifer

Species		Instar 1	2	3	4	5
O. furcifer .	Size					
	Length	0·42–0·60	0·60–0·84	0·84–1·05	1·05–1·29	1·29–1·50
	Head width (mm)	0·12–0·15	0·15–0·21	0·21–0·24	0·24–0·27	0·27–0·30
	Time for development in weeks					
	(mean)	1·5	3·1	5·1	9·2	12·9
	(standard deviation)	0·52	0·35	1·16	1·82	1·64
O. latus .	Size					
	Length	0·63–0·78	0·78–1·05	1·05–1·20	1·20–1·50	1·50–2·10
	Head width (mm)	0·15–0·18	0·18–0·24	0·24–0·30	0·30–0·36	0·36–0·42
	Time for development in weeks					
	(mean)	1·0	5·2	7·5	13·5	22·8
	(standard deviation)	0	1·32	1·43	2·90	2·84
O. procampatus .	Size					
	Length	0·60–0·78	0·78–1·11	1·11–1·29	1·29–1·65	1·65–1·95
	Head width (mm)	0·15–0·18	0·18–0·21	0·21–0·24	0·24–0·27	0·27–0·30
	Time for development in weeks					
	(mean)	2·3	7·7	10·9	16·9	23·5
	(standard deviation)	0·98	2·81	2·89	2·40	4·03

maturity was attained in the fourth instar, 9–12 weeks from hatching, at 12° C. Mortality was very high at 24° C. and only two individuals were successfully reared under these conditions. Growth of the survivors at 24° C. was approximately equal to growth at 12° C. Eggs were not laid at 24° C. At 12° C., and assuming the sex ratio 1 : 1 in a culture of 20 specimens, each female laid a mean of eight eggs.

Onychiurus latus Gisin

This species is distinguished by the presence of yellow pigmentation. It is considerably larger than *O. furcifer*, mature specimens measuring more than 1·5 mm., and is found in the humus and upper soil layers. It is similar to other Onychiuridae in the lack of eyes and furca. The eggs were laid singly or in small groups on the surface of the culture medium and measure 0·24–0·25 mm. in diameter before development. The diameter increases to 0·26 mm. before hatching. Development time from laying to hatching was 19–22 days at 12° C. and 8–10 days at 24° C. The size of newly hatched specimens was 0·60–0·72 mm. in length and 0·15 mm. in head width. Individual measurements of ten individuals were made at 12° C. Four ecdyses occurred before sexual maturity ; development time is shown in Table II. Pigment

was developed in the second instar. Eggs were laid 16–23 weeks after hatching. There was no egg-laying at 24° C. and young individuals survived for only one to three weeks at this temperature. At 5° C. egg development did not take place. Eggs were laid by mature specimens after 27 weeks at this temperature. At 12° C. a mean of six eggs was laid by each female in a culture of 60 mature specimens if the sex ratio is assumed to be 1 : 1. Under laboratory conditions at 12° C. survival for 12 months is common. At 5° C. seven individuals out of 40 adults survived for 12 months.

Onychiurus procampatus Gisin

This species is closely related to *O. latus* but is slightly smaller and unpigmented. The eggs are similar to those of *O. latus* in appearance and only slightly smaller in size and were laid singly or in pairs on the surface or in cavities of the culture medium. Embryonic development was slower than in *O. latus*, ranging from 31to 33 days at 12° C. No development took place at 5° C. or 24° C. Newly hatched specimens measured 0·60–0·66 mm. in length and 0·15 mm. in head width and were otherwise similar to mature specimens in appearance. The post-embryonic development of 15 individuals was observed and measured and the results are shown on Table II. Egg laying commenced in the fourth instar, 18–22 weeks after hatching.

In laboratory cultures at 12° C. the original adults have been found to survive for more than 12 months. In cultures at 5° C. 27 individuals survived after 12 months from 40 originally introduced.

Folsomia candida Willem

F. candida is an unpigmented, blind species of the family Isotomidae, with a well-developed furca. It has an active running movement and springs readily if disturbed. Under bracken it has been found by the author to be evenly distributed between the humus and upper true soil layers. The eggs measure 0·11–0·13 mm. in diameter and are otherwise similar to those of the species of *Onychiurus* which were studied, though less opaque. They were laid in groups of 9–36, with a preference for cavities in the plaster medium with an external aperture less than 0·5 mm. in diameter. There is a tendency for oviposition at the same site by a number of individuals so that large egg masses are formed. At 5° C. development of the egg took 90 days, at 12° C. 13–15 days and at 24° C. 7–9 days. Newly hatched individuals were almost transparent and measured 0·30–0·35 mm. in length and 0·09 mm. in head width, but were otherwise similar to the adult. The very active habits of these insects and other considerations prevented the making of direct observations of the growth of individuals. Estimates of growth by measuring ten individuals at intervals from cultures at 12° C. and 24° C. are shown in Table III. At 12° C. eggs were laid 30–40 days after emergence ; at 24° C. maturity was attained after 20–24 days from hatching. A mean per mature female of 29 eggs at 5° C., 22 at 12° C. and 30 at 24° C. was laid in the two weeks after maturation.

TABLE III.—*Growth of* Folsomia candida *in cultures at two temperatures.* (*Means of measurements of* 10 *individuals*)

	Days from emergence										
	1	3	5	8	10	15	19	22	28	33	38
12° C.—											
Length (mm.)	0·33	0·34	0·45	0·44	0·44	0·54	0·59	0·60	.	0·68	0·69
Head width (mm.)	0·09	0·09	0·10	0·11	0·11	0·13	0·14	0·15	.	0·16	0·17
24° C.—											
Length (mm.)	0·34	.	0·41	0·49	0·69	0·69	.	.	0·88	.	.
Head width (mm.)	0·09	.	0·10	0·12	0·16	0·17	.	.	0·21	.	.

Isotoma viridis Bourlet

This species is a large (over 2 mm.) member of the family Isotomidae with well-developed pigmentation and furca. It runs actively and has also a very strong springing movement when strong stimulus is applied. Adults were found mainly in the upper humus layers under bracken and it can be taken as typically a surface-dwelling form.

The eggs are smooth surfaced, globular, measuring 0·21 mm. in diameter before development, with pale red pigmentation, and the mature female lays one clutch of 27–54 eggs. Oviposition was always on the surface of the culture medium. Development of the eggs did not take place at 5° C. ; at 12° C. development to hatching lasted 16–20 days and at 24° C., 6–9 days. The newly hatched young measure 0·57–0·63 mm. in length and 0·15 mm. in head width. A red pigment, possibly carotenoid in nature, is present in the body fluid of this species and gives the young a pale red coloration. Surface pigmentation becomes apparent only after the first ecdysis. Attempts to rear this species to maturity were unsuccessful.

Neanura muscorum (Templeton)

This is also a large species with a maximum length of over 2 mm. and with dark pigmentation. Movement tends to be rather slow and ponderous ; it was found under bracken on the surface humus layer. The eggs are comparatively large, measuring 0·28 mm. in diameter before development and 0·39 mm. in greatest diameter before hatching. They are globular, with a lightly marked surface, and cream coloured. Mature females were found to lay six to ten eggs either singly or in pairs on the surface of the culture medium. Development of the egg at 12° C. lasted 24 days, and at 24° C. 12–13 days. No development took place at 5° C. The newly hatched insects measured 0·63–0·75 mm. in length and 0·24 mm. in head width, and have a pale grey-brown " ground " pigmentation with pale purple pigment on the head and darkly pigmented eyes. At 12° C. purple surface pigment became obvious after eight days and developed progressively ; at 24° C. pigment was less well developed in the young. Growth did not take place at either temperature and maximum survival of young was 70 days at 12° C. and 30 days at 24° C. The failure was possibly due to lack of suitable food material. The mouthparts differ from those of the other species investigated, and this probably indicates a difference in feeding habits (MacNamara, 1924).

Discussion

Comparable investigations of the life histories of arthropleone Collembola are few, the species concerned being *Hypogastrura manubrialis* (Tullb.) by Ripper (1930), *H. purpurascens* (Lubb.) by Strebel (1932), *Orchesella cincta* (L.) by Lindemann (1950) and *H. armata* Nic. by Britt (1951). A summary of some of their results is given in Table IV.

Ripper's (1930) investigation of *H. manubrialis* was prompted by the economic importance of this insect in causing damage to mushroom beds. The mature female is reported to lay eggs in groups of approximately 30 in cavities in the soil. The young were unpigmented but otherwise similar to the adult. Ecdyses were observed every five to seven days and sexual maturity was attained five to seven weeks after laying, but environmental conditions for post-embryonic development are not reported. A suggestion that parthenogenesis occurs is deduced from the fact that a high proportion of females (which Ripper (1930) was able to distinguish from males) was found in the cultures.

Strebel (1932), in his study of *Hypogastrura purpurascens*, obtained similar results for the life of this species. In both investigations " moulting societies " are reported in which groups of individuals are formed and moulting takes place

TABLE IV.—*Summary of results of previous life-history studies*

	Egg-laying				Development					
					Embryonic days		Post-embryonic days		Number of ecdyses before maturity	Length of newly hatched insect (mm.)
	Colour	Shape	Size (mm.)	Number	10° C.	22° C.				
Hypogastrura manubrialis (Tullb.) (Ripper, 1930)	White	Globular	0·18	30	36	19	35–49		6 (every 5–7 days)	0·49
H. purpurascens (Lubb.) (Strebel, 1932)	„	„	0·18	20–30	19	28	42–49		5 (every 4–15 days)	
					12° C.	24° C.	12° C.	23° C.		
Orchesella cincta (L.) (Lindemann, 1950)	„	„	0·20–0·25	.	21	8	160–180	40–60	10–12	0·4–0·5
						24° C.		24° C.		
H. armata Nic. (Britt, 1951)	„	„	0·16	28	.	8	.	15–19	3–4	0·14

practically simultaneously. This behaviour was not observed in any of the species investigated in the present study. The work of Britt (1951) on *H. armata* suggests that this species is also similar in development to the other members of the genus previously investigated, although development time is somewhat shorter. Females are reported to reach maturity, in the third to fourth instar, in 23–27 days at 24° C. In all three species the appearance and size of the eggs and number laid are in close agreement.

The investigation by Lindemann (1950) of *Orchesella cincta* showed the relation of temperature to rate of development of the egg, which ranged from 21 days at 12° C. to eight days at 24° C. For another species, *O. villosa* (L.), the pre-maturation period is said to last 30–50 days at 22–23° C. and 130–180 days at 10–12° C. Young individuals of *O. cincta* have diffuse violet " ground colour " and surface pigmentation during the 10–13 instars reported before maturity. The development of pigment in this species appears to be similar to that of *Isotoma viridis* and *Neanura muscorum*.

The method of sperm transfer was not observed in any of these studies and our knowledge is limited to the report by Schaller (1953) that in the species *Orchesella villosa* and *Tomocerus vulgaris* (Tullberg) spermatophores are deposited on the surface of the substrate. The females are then said to place the abdomen in contact with one of the spermatophores before eggs are laid. Schaller (1953) also reports that no eggs were laid by isolated females, and this tends to confirm that parthenogenesis does not occur. In the present work there was no egg-laying before introduction of the insects into a communal breeding dish. Investigation of the culture medium in the breeding dishes, however, did not reveal the presence of structures similar to the spermatophores described by Schaller (1953).

The embryonic development times of the species in the present study show the same order of magnitude (two to five weeks at 12° C., see Table V) as do previously reported records of development of Collembola. Raising the temperature to 24° C. approximately halves the development time, as might be expected from chemical considerations. The length of time for post-embryonic development of *F. candida* and *T. krausbaueri* is similar to that reported for *Hypogastrura* spp. (Ripper, 1930; Strebel, 1932; Britt, 1951) but the other species studied have a

TABLE V.—*Summary of results of present study*

	Egg-laying					Development							
						Embryonic			Post-embryonic			Size of young (newly hatched) (mm.)	
Species	Colour	Shape	Size (mm.)	Number	Mean number per female during life	5° C. (Days)	12° C. (Days)	24° C. (Days)	12° C. (Days)	24° C. (Days)	Number of ecdyses before maturity	Length	Head width
T. krausbaueri	White	Globular	0·09–0·10	1–2	10	.	15–20	.	30–40	.	3	0·24	.
O. furcifer	„	„	0·17–0·19	1–6	8	.	26–30	11–15	63–84	.	4	0·42	0·12
O. latus	„	„	0·24–0·25	1–2	6	.	19–22	8–10	112–161	.	4	0·63	0·15
O. procampatus	„	„	0·23	1–2	7	.	31–33	.	126–154	.	4	0·60	0·15
F. candida	„	”	0·11–0·13	9–36	22–30	90	13–15	7	30–40	20–24	.	0·33	0·09
I. viridis	Pale red	„	0·21	27–54	45	.	16–20	6–9	.	.	.	0·57	0·15
N. muscorum	Cream	„	0·25–0·29	1–2	6–10	.	24	12–13	.	.	.	0·69	0·24

much longer post-embryonic development time (9–23 weeks at 12° C.) which is close to the results reported by Lindemann (1950) for *O. villosa* (18–26 weeks at 12° C.). The post-embryonic development times for *I. viridis* and *N. muscorum* are probably also of this order of magnitude.

The results obtained are interesting if studied in conjunction with the data of seasonal variation reported elsewhere (Milne, 1959). At 12° C. the complete life cycle of *T. krausbaueri* lasts seven to nine weeks, of *F. candida* six to eight weeks, of *O. furcifer* 13–16 weeks and of the other *Onychiurus* species, 19–27 weeks. Under climatic conditions prevailing at Milngavie it might be expected that those species with longer life cycles are unlikely to produce more than two generations in one year and with low winter temperatures may be restricted to one generation. This is reflected to some extent in the field results; for example, *I. viridis* shows a single yearly peak in population, *O. procampatus* has a twice yearly peak and *F. candida* an irregular variation suggestive of a short life cycle and more rapid change of population size in response to external factors. Suitable temperatures for the development of the species studied here lie between 5° C. and 24° C. The effect of the lower temperature, although slowing down and preventing reproduction in many species, nevertheless ensures a fairly stable level of population. The high temperature, although increasing the rate of development of some species, causes such a high mortality rate (except in *F. candida*) that reduction in the population would be expected if subjected to this temperature for more than a few days.

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Book Notice

Horticultural Pests. Detection and Control. By G. Fox Wilson. *New ed.* revised by P. Becker. 8vo. London (Crosby Lockwood & Son), 1960. Pp. xix, 240 : text illust, 25*s*.

This work is a revision of *Detection and Control of Garden Pests*, published in 1947, with its scope enlarged and title changed to correspond, nomenclature brought up to date and new pests included. The illustrations have been improved and increased in number and a new chapter on damage to lawns has been added. In addition to a general index, there is an index of host plants, giving symptoms of attack, and an index of pests, giving their main host plants.

The work is designed for those whose knowledge of plant pathology is limited and who require guidance in recognizing animal organisms primarily responsible for crop injury and who need advice on avoiding and controlling pest outbreaks. The contents are divided into chapters, corresponding to the main parts of plants, in which their signs of attack are described under sections arranged alphabetically and listed under the head of each chapter. Months are given after the names of most pests to indicate when damage by them is to be expected.

THE DISTRIBUTION OF BEES IN A HONEY-BEE (*APIS MELLIFERA L.*) COLONY

By J. B. Free

(*Rothamsted Experimental Station*)

Introduction

Nurse bees give larvae food which comes partly from their hypopharyngeal glands (*see* Ribbands, 1953) and mandibular glands (Barker *et al.*, 1959 ; Callow *et al.*, 1959). Several workers (*e.g.* v. Planta, 1888–9 ; Vivino *cited* Haydak, 1943 ; and Shuel & Dixon, 1960) have analysed the food given to queen and worker larvae of different ages. Although somewhat variable results have been obtained, taken together they indicate consistent differences in the part of the food derived from the glands given to queen larvae, young worker larvae and old worker larvae. If so, either (*a*) a nurse bee can feed a larvae of any age but varies the composition of its glandular secretion to suit the one being fed, or (*b*) the composition of the glandular secretion varies in different workers, independent of age, and each only feeds those larvae to which its secretion is suited, or (*c*) the glandular secretion and category of larva fed changes as the nurse bee becomes older. Rösch (1925, 1930) and Perepelova (1928) obtained some evidence in support of the last of these alternatives. This problem has been reinvestigated by comparing the distribution of bees of known ages on combs containing brood of known ages.

Methods and Results

Groups of newly emerged marked bees were introduced at intervals to each of two colonies, and the queen of each was confined on a comb in a cage of slotted metal sheet through which workers, but not queens, could pass. Every three days an empty comb was substituted for the one containing the eggs laid by the queen so that a series of combs containing brood of different ages was obtained.

In each hive the combs were parallel to the entrance and in two chambers one above the other. In one the combs were arranged so that the brood increased in age from the back to the front of the lower chamber, whereas in the other the youngest brood was in the centre of the lower chamber and increased in age towards the ends. In each hive combs containing honey and pollen were placed at either end of the lower chamber and throughout the upper chamber.

To determine the distribution of the marked bees, the hives were opened (2nd August) when relatively few bees were flying. The combs with adhering bees were quickly removed with the minimum of disturbance ; each was enclosed in a separate box and the contents of each subsequently examined in an insectary. The results from both colonies were similar and are presented together (Table I). Bees are assumed to have been one day old when introduced to the colonies.

With increase in age, a bee was the less likely to be found on larval combs and more likely to be found on storage combs in the upper chamber. The distribution of bees on sealed brood did not vary with their age. The relatively large percentage of young bees found on the storage combs in the lower chamber is probably associated with their high pollen requirements when brood feeding. Most of the young bees (2–11 days old) on storage combs in the lower chamber were at the back and only few at the front near the hive entrance (100 and 28 respectively), whereas the older bees (15–36 days old) were more uniformly distributed (12 and 17 at back and front respectively). Most bees which returned to the empty hives after removal of the

TABLE I.—*Percentage distribution of bees of different ages* (*No. of bees given in brackets*)

	Contents of combs								
	Brood combs						Storage combs		
Number of combs Age of bees (days)—	1- and 2-day-old eggs 2	3-day-old eggs and 1- and 2-day-old larvae 2	3-, 4- and 5-day-old larvae 2	6-day-old larvae and recently sealed brood 2	Sealed brood 4	Sealed and emerging brood 4	Stores in lower chamber 7	Stores in upper chamber 24	Number of bees returned from flight after removal of combs
2 and 3 . .	10·5 (25)	12·6 (30)	13·4 (32)	5·5 (13)	13·0 (31)	10·1 (24)	18·1 (43)	16·8 (40)	4
4 and 5 . .	6·0 (8)	9·7 (13)	9·0 (12)	7·5 (10)	14·2 (19)	10·4 (14)	26·9 (36)	16·4 (22)	10
8 and 11 . .	9·0 (19)	8·1 (17)	6·7 (14)	6·2 (13)	13·8 (29)	8·1 (17)	23·3 (49)	24·8 (52)	37
15 and 18 . .	3·2 (3)	5·4 (5)	7·5 (7)	7·5 (7)	5·4 (5)	5·4 (5)	21·5 (20)	44·1 (41)	36
22, 25, 29, 33 and 36	6·3 (5)	1·3 (1)	5·1 (4)	3·8 (3)	11·4 (9)	13·9 (11)	11·4 (9)	46·8 (37)	75

TABLE II.—*Development of hypopharyngeal glands of bees on various types of comb*

Contents of combs	1- and 2-day-old eggs	3-day-old eggs and 1- and 2-day-old larvae	3-, 4- and 5-day-old larvae	6-day-old larvae and recently sealed brood	Sealed brood	Sealed and emerging brood	Stores in lower chamber	Stores in upper chamber	Bees returned from flight after removal of combs
Number of bees examined .	57	62	69	45	86	71	150	170	160
% with developed glands (stages 4, 5 or 6)	61·4	71·0	73·9	62·2	69·8	78·5	78·0	48·8	40·3
% with undeveloped glands (stages 1 or 2)	14·0	4·8	2·9	13·3	12·8	11·4	11·3	31·2	46·0

combs were older bees. The numbers of bees of different ages counted flying from the hives the previous day were : 2–3 days old, 0 ; 4–5 days old, 6 ; 8–11 days old, 15 ; 15–18 days old, 21 ; 22–36 days old, 65.

There was an approximately equal distribution of bees of each age group on the combs containing young larvae, old larvae, and eggs. Considering the numbers of the different types of comb present it is apparent that :—(*a*) there were more bees up to 18 days old per comb of larval brood than per comb of sealed brood (2 & 3 day old bees, $P<0{\cdot}001$; 15 & 18 day old bees, $P<0{\cdot}05$) ; (*b*) there were more bees up to 11 days old per comb of sealed brood than per storage comb (2 & 3 day old bees, $P<0{\cdot}001$; 4 & 5 day old bees, $P<0{\cdot}001$; 8 & 11 day old bees, $P<0{\cdot}01$) ; (*c*) bees of 22 days and older did not show any comb preferences.

The hypopharyngeal glands of the bees collected were classified into 6 arbitrarily defined stages of development, of which 1 and 2 are considered undeveloped and 4, 5 and 6 developed. The results for the different combs are given in Table II.[1] The lowest percentages of bees with undeveloped hypopharyngeal glands were on the larval combs, whereas the highest percentages with developed hypopharyngeal glands were on stores in the brood chamber, on combs of sealed and emerging brood and on larval combs. This distribution is the one expected and tends to confirm that the normal distribution of bees, of different occupations, within the hives was not appreciably disturbed during the collection of combs and bees.

TABLE III.—*Distribution of marked bees in normal colonies*

	Age of bees (days)			
	1	4 and 5	7 and 8	11 and 12
Number of bees . .	1112	862	685	607
% on brood combs .	74·0	63·2	53·7	51·7
% on storage combs .	26·0	36·8	46·3	48·3

	Age of bees (days)			
	14 and 15	17 and18	24	31
Number of bees . .	320	223	83	38
% on brood combs .	55·6	43·5	36·1	15·8
% on storage combs .	44·4	56·5	63·9	84·2

Further information was obtained by introducing newly emerged marked bees to normal colonies and recording the numbers found on brood and storage combs at intervals afterwards. The results of seven such series of observations are combined in Table III. The distribution of the bees on the two types of combs was similar to that recorded above.

DISCUSSION AND CONCLUSIONS

Because there was no difference in the distribution of nurse bees of different ages on combs of young and old larvae, it is improbable that nurse bees of different ages feed larvae of different ages. The significance Rösch (1925, 1930) and Perepelova (1928) placed on their evidence that younger workers feed older larvae, and older workers feed younger larvae may have been coloured by their belief that older larvae are fed solely on pollen and honey, and that when feeding them the young workers eat some of the pollen with the result that when about six days old their hypopharyngeal glands have developed sufficiently for them to feed the younger larvae. However,

[1] Storing the bees in Pampel's fluid discoloured their paint marks and so prevented determination of their ages.

the amount of nitrogen supplied by the pollen eaten by a larva is small (Simpson, 1955) in comparison with the total nitrogen required during the fourth and fifth days of larval life (Melampy *et al.*, 1940), so it is apparent that larvae are fed on glandular secretion throughout their development.

Moreover, it is doubtful whether Rösch and Perepelova would always have succeeded in differentiating clearly between a bee that was feeding a larva, and one inspecting it or merely resting in the larval cell (*see* Lindauer, 1953).

Lindauer (1953) found that in a small colony an individual worker may feed larvae of widely varying ages during a single day. However, because he also found that during its development a larva is fed by about 143 bees, any differences in the composition of the glandular secretion fed to young and old larvae could result from different proportions of young and old nurse bees feeding them. If so, this would be expected to be reflected in the present population studies. Lindauer's observations, together with the results of this work, indicate that, either an individual bee can vary the composition of the glandular secretion it feeds to suit the age of the larva concerned, or, less probably, the glandular secretion differs in individual bees irrespective of their age.

It is hoped that the results obtained will be useful in elucidating and developing various beekeeping practices in which knowledge of the distribution of bees of different ages is desirable.

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THE INVASION OF BRITAIN BY *CIS BILAMELLATUS* FOWLER (COLEOPTERA : CIIDAE)

By Kitty Paviour-Smith

(*Bureau of Animal Population, Oxford*)

(Communicated by C. S. Elton, F.R.S.)

Discovery and Spread

" I have much pleasure in recording the capture of this most singular insect, which, as it appears to be unknown on the Continent, I venture to describe as new to science. I have met with it on three occasions during the present year. Firstly, a single male specimen, beneath the bark of a decaying pine tree, on January 23rd ; secondly, September 15th, in utmost profusion, from boleti upon a decaying birch ; and thirdly, September 23rd, a single male from a large fleshy fungus upon an ash tree, a mile and a half from the scene of the former captures. All three localities are at West Wickham, and it is astonishing that so conspicuous an insect should have been passed over for so long, more especially in a district which has been worked over by some of our best collectors ".—*Rev. Theodore Wood* (1884) *recording the first discovery anywhere in the world of the ciid beetle,* Cis bilamellatus *Fowler.*[1]

This beetle has become of ecological importance in England as an invader of, and the most efficient destroyer of, a very common minor habitat, namely dead dry fruiting-bodies of the " birch-bracket " fungus, *Polyporus betulinus* (Bull.) Fr.[1]

1884–1903[2] *:* During the 20 years that followed its discovery *Cis bilamellatus* was recorded only once, in 1891 from Mitcham in Surrey, only a few miles from West Wickham.

1904–23 : The next 20 years of its history in this country opened with its rediscovery, only half a mile from the type locality, by the original discoverer, and at Shirley Common, Surrey, by H. Donisthorpe and later by E. C. Bedwell. During this period the species remained local in the London area ; it was collected and recorded from Surrey, Kent, Middlesex and Hertfordshire. There is only one record for a region beyond the London area, and since this may be regarded as doubtful it has not been entered on the map. G. C. Champion (1910) wrote, " During the present winter it [*Cis bilamellatus*] has been found breeding in great numbers in *Polyporus* on birch, obtained from the New Forest by one of our local [London] natural history dealers . . . not been recorded from the New Forest, and the insect may have found its way into the stocked *Polyporus* from some obtained from other places ".

1924–33 : Records and collections within the next decade are all from within the same area, with the addition of Windsor Forest, on the eastern edge of Berkshire, and Arundel, in Sussex. Thus, for at least 50 of the 75 years of its recorded history in Britain, *Cis bilamellatus* was taken only from the London area.

1934–43 : The records for the following ten years, however, show a sudden extension of range, though it seems highly probable that the species had been spreading unnoticed for some time. It was recorded for Watlington, in Oxfordshire, in 1936, and from places as far north as Nottinghamshire in 1938 and Cheshire in 1942.

The apparent suddenness with which the species spread, since, say, 1924, may in fact be connected with a changed distribution of coleopterists who were interested either in this obscure beetle family or in collecting from the fruiting-bodies of macrofungi, but G. W. R. Bartindale (*personal communication*) " did a large amount of

[1] Nomenclature of insects according to Kloet and Hincks (1945) and of fungi according to Rea (1922).

[2] The records for these and the following periods have been assembled in Appendix I and figure 1.

collecting in the Macclesfield area from 1932 to 1939 and got a good number of fungus-feeding beetles without finding *C. bilamellatus* ", and J. J. Walker was regularly adding supplements to his published list of Oxfordshire Coleoptera, and in his sixth supplement in 1929 he had still not recorded *C. bilamellatus*, nor had he done

Fig. 1.—The spread and present known distribution of *Cis bilamellatus* Fowler.
○, recorded absences. – – ● – –, furthermost records for each period, linked by dotted lines to show apparent spread. **1**, 1884–1903; **2**, 1904–23; **3**, 1924–33; **4**, 1934–43; **5**, 1944–53; **6**, 1954–59.

so for the " Oxford District " up to 1938. On the other hand, this extension of range may be associated with some comparatively sudden and widespread change in the abundance or distribution of its preferred habitat, *Polyporus betulinus*.[3] Macdonald (1937) says that " In Scotland it is the most common fungus on birch. Judging from records of about 100 years ago it seems that the fungus is becoming increasingly common. Greville (1826) stated that it must be of infrequent occurrence. Some 50 years later Stevenson (1879) recorded it for all the divisions of Scotland except that which he designates ' Sutherland '. The present writer has found the fructifications abundant wherever birch grows in Scotland . . . The large amount of the fungus present in Scotland is undoubtedly due to the lack of attention paid to the host trees ".

It is possible that in England, too, the fungus may have become increasingly common. This may have been due to the neglected state of many forests after the First World War, or to climatic effects which perhaps left trees more vulnerable to infection, but this is pure speculation.

The beetle will, however, live in certain other fungi when they die.[4] It has been found breeding in *Polyporus adustus* (Willd.) Fr. several times, and on one occasion each in the following fungi : drying *Polyporus squamosus* (Huds.) Fr. (E. Lewis, *personal communication*), *Ganoderma applanatum* (Pers.) Pat., an unidentified species of *Irpex*, *Polystictus hirsutus* (Wulf.) Fr. and *Pleurotus sapidus* Schulz. In addition, specimens have been found on rare occasions in *Polyporus sulphureus* (Bull.) Fr. (J. L. Henderson, *personal communication*), *Polystictus versicolor* (L.) Fr., *Trametes gibbosa* (Pers.) Fr. and *Fomes annosus* Fr. (*see* Appendix I). However, in any attempt to trace the distribution of this beetle, it seems simplest to examine first the fungus which is known to be its preferred " headquarters " (*Polyporus betulinus*), if it occurs in the area. The other fungi are probably stepping-stones for the beetle species in the absence of *P. betulinus*.

1944–53 : E. Milne-Redhead took the beetle in 1944 in several localities in Bedfordshire and Buckinghamshire, and there are records later of captures in Sussex, Cambridgeshire, Hampshire, and new localities in Cheshire and mid-Berkshire.

1954–59 : Records have been added for Essex and eastern Kent, and this paper (Appendix I) records the addition to the known distribution of the beetle of localities in Yorkshire, Lincolnshire, Leicestershire, Huntingdonshire, Norfolk and Suffolk in the region north of London ; in Glamorgan, Gloucestershire, Wiltshire and Dorset in the west ; and in the Isle of Wight in the south.

Regions To Which The Beetle Has Not Yet Spread

Distribution maps tend to reflect the distribution of collectors or the travels of the authors more clearly than they reflect the actual distribution of the plant or animal concerned. Figure 1, however, shows not only the spread and present known distribution of *C. bilamellatus* in this country, but also localities from which collections (sometimes large) of dead *Polyporus betulinus* have been carefully examined but no specimens of this beetle species found. Details of these collections are given in Appendix II.

Collections from Banffshire, Aberdeenshire, Inverness-shire, Angus, Kincardine, Perthshire, Fife, Dunbarton and Midlothian indicate that the species has not yet reached Scotland.

Fairly extensive collections from North Lancashire and Westmorland have not yet shown the beetle to be present in the north-west of England, while collections from Durham and Northumberland indicate its absence there too. Absence from

[3] Paviour-Smith (1959, 1960) ; also detailed habitat data, collected by the author and deposited in the Bureau of Animal Population, Oxford.

[4] See previous footnote.

a single fruiting-body from the North Riding of Yorkshire is considered insufficient evidence, especially since the beetle has now been taken from Skipwith Common, just south of York.

In the west, it has been taken in extensive collections in east Dorset, but it was absent from a large collection from Yarner Wood, in Devon.

Only two small collections of dead old *Polyporus betulinus* have as yet been available from Wales. *Cis bilamellatus* was absent from Caernarvonshire but present in Glamorgan, and too little material from the mid-west has been examined for any conclusion to be reached about its real western limits. The beetle was not present in a collection from the Forest of Dean, but this may have been because only three of the fungi examined were dead and, since they had only just died, colonisation may not yet have occurred. The beetle was also absent from very small collections from western and north-western Worcestershire.

It is clear, therefore, that most of the negative evidence available so far is for the north. North of its range is the densely populated industrial country in the west, and in the middle the mostly open limestone country of the Yorkshire moors with very little birch. Perhaps lack of sufficient suitable habitat may so far have prevented the continued northward spread of *Cis bilamellatus*. Its possible distribution may, however, be determined by climatic factors, and it is also conceivable that the present northern limit is, in fact, only a temporary frontier.

The Origin of *Cis bilamellatus*

It has already been seen with what surprise the Rev. Theodore Wood greeted the appearance in 1884 of " so conspicuous an insect . . . in utmost profusion " in an area that had been " worked over by some of our best collectors ". Moreover, this insect was " unknown on the Continent ", when most of the British and European species of the family had already been described. It seems likely, therefore, that it was an introduction to this country.

In 1910, G. C. Champion, having examined the collections of Ciidae in the British Museum (Natural History), pointed out that *Cis bilamellatus* Fowler, 1884, was synonymous with *Cis munitus* Blackburn, 1888, whose type locality was Port Lincoln, South Australia. It seems that *C. bilamellatus* must have been introduced, probably accidentally, from Australia. Champion suggested that it had also been introduced into Australia from some unknown home, but since it has been taken there from such widely separated regions as Port Lincoln in South Australia (before 1888), Ryde in New South Wales (1901), Hobart in Tasmania (before 1917), New Holland and South Morang in Victoria, and King George's Sound and Albany in Western Australia, it seems much more likely that that country was its original home.

Since 36 of the habitat records (excluding my own specialised collecting) have been from the fruiting-bodies of macrofungi, and only the remaining eight from under bark, usually fungus-infested (Appendix I), it seems that the beetle is more likely to have reached this country within a fungus fruiting-body than in any other way. It is to be found in abundance only in this habitat.

Who, but mycologists sending herbarium specimens, would be sending such material halfway across the world? Since London was the centre of the beetle's spread, and also possessed two of the oldest and most important herbaria in the country, it seemed feasible to look first to Kew and the British Museum (Natural History).

The next problem is in what species of fungus would one expect the beetle to have arrived? One of its habitats in Australia is apparently *Trametes cinnabarina* (Jacq.) Fr., since eight specimens on one card (under the name of *Cis bilamellatus* Fowler) in the National Museum of Victoria were taken in this fungus (under the name of *Polystictus cinnabarinus*) from South Morang, Victoria (information from A. N. Burns,

National Museum of Victoria), but no other specimens in British or Australian Museums have any habitat data. However, its preferred habitat in Britain is *Polyporus betulinus* which is a much softer and more friable fungus than *Trametes cinnabarina*. The latter, according to Cunningham (1947), is structurally very near to *P. versicolor*, a fungus in which the beetle is *very* seldom found in this country.

A clue about a possible native " preferred headquarters " for *Cis bilamellatus* may, however, be found in the following quotation from Cartwright and Findlay (1946). " *Polyporus betulinus* is widely distributed and common in Europe, Asia and America, occuring wherever birches are grown. It has been reported from Australia, but Lloyd (1915) states that in that country it appears to be represented by the closely related *P. eucalyptorum* ". This suggested that *Polyporus eucalyptorum* Fr., if like enough to *P. betulinus* to have been at first confused with it by botanists, might be sufficiently similar to it in structure, texture and other ways to have been the native preferred habitat of *Cis bilamellatus*. Cunningham (1948) also emphasises that this fungus species closely resembles *P. betulinus* (possessing a similar cuticle and the same type of hyphae, and differing only in minor ways). He points out that *Polyporus portentosus* Berkeley and *P. eucalyptorum* Fr. are one and the same species, and that " Berkeley's specific name has priority, and should replace *P. eucalyptorum*, of which there is no extant type ". Examination of a complete dried specimen of *P. portentosus* in the Kew Herbarium showed the author that this species is indeed very similar to *P. betulinus* in texture and friability. It therefore seemed worthwhile examining herbarium specimens of *P. portentosus* in both Kew and the British Museum (Natural History) for signs of beetle damage, dates of importation and localities in Australia.

Out of eight specimens of *P. portentosus* fruiting-bodies from Australia in the Kew Herbarium, seven showed damage by fungus beetles. Four of these had obviously been damaged by large beetles, but three had small galleries of just such a size as those made by *Cis bilamellatus*. The type specimen of the fungus is a heap of beetle-ruined dust!

A number of specimens of *P. portentosus* did come into the country about halfway through last century. Berkeley, living at King's Cliff, Northamptonshire, received the type in 1843, described it in 1844, and his specimens went to Kew in 1879. Various other specimens were imported between 1843 and 1845, and one collection, at least, reached Kew in 1865 (*information from Dr. R. W. G. Dennis*). It is possible that Kew found some of the specimens too beetle-ridden, and some were thrown away, although apparently no record of this would have been made.

The British Museum (Natural History) contains two specimens of the fungus from Australia. Both show beetle damage, but this appears to the author to be rather too big to have been caused by *Cis bilamellatus*. (Mrs. F. L. Balfour-Browne considered that the galleries might well have been made by the " herbarium beetle ", *Stegobium paniceum* (L.).) The specimens were received by Berkeley and Broome between 1878 and 1882, and came into the hands of the museum in 1886.

Furthermore there is direct evidence that ciids have been known to enter this country in herbarium material. When Pool (1917) was describing *Cis lineatosetosus*, he traced the specimens of this species in British collections to beetles taken from " a fungus from the South Sea Islands that had been many years in the Mus. Brit. (alive). From W. Carruthers, Esq., Sept. 1866 ". He guessed (*loc. cit.*) that *Cis bilamellatus* might also have entered this country in this way from Australia.

Again, Scott (1927) describes finding the European *Rhopalodontus bauderi* Abeille breeding in a specimen of *Fomes fomentarius* (Linn.) Fr., in the Cambridge Forestry School in 1924. The fungus had come from Landes, in France.

It seems very likely, therefore, that during the last century herbarium specimens of fungi were not always as carefully fumigated as they now are, and that these were the probable source of introduction of this most interesting invader, *Cis bilamellatus*.

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APPENDIX I

Localities for which there are records of *Cis bilamellatus*

Only the first record for any locality is given.
The table is arranged strictly in chronological order.

Abbreviations :

* The author, searching for *Cis bilamellatus*, examined these fruiting bodies.
+ These records show the outer limits of the known distribution of *Cis bilamellatus* for the periods shown in figure 1.
B.A.P. records, Bureau of Animal Population records.
nil, no published records.
pers. comm., personal communication.
B, under bark.
F, in unnamed fungus (" boleti " on trees usually means " polypore ").

F.a., Fomes annosus.
G.a., Ganoderma applanatum.
I, Irpex sp.
P, unnamed *Polyporus* sp. (probably *P. betulinus* if on birch).
P.a., Polyporus adustus.
P.b., Polyporus betulinus.
P.s., Pleurotus sapidus.
P. sq., Polyporus squamosus.
Pst., Polystictus sp.
Pst. h., Polystictus hirsutus.
T.g., Trametes gibbosa.

Year	County and locality	Collector	Habitats	Source of information
+1884	Kent, West Wickham Wood	T. Wood	? *P* on birch, B, F	Wood (1884).
+1891	Surrey, Mitcham	Mr. Heasler	F	[Heasler] (1891).
1904	Surrey, Shirley Common	H. Donisthorpe	F	Donisthorpe (1904).
+1911	Surrey, Chipstead	?	?	Norwich Museum ; nil.
+1916	Surrey, Richmond Park	H Donisthorpe	?	Hope Museum, Oxford ; Pool (1917).
+1917	Kent, Orpington	C. J. C. Pool	?	Pool (1917).
+1917	Middlesex, Highgate	Janson	?	Pool (1917).
+1917	Surrey, Losely Park, nr. Guildford	G. C. Champion	*P* on lime	Champion (1917).
+1918	Surrey, Reigate	A. M. Massee	?	pers. comm. ; nil.
1920	Surrey, Mickleham Downs	A. M. Massee	?	pers. comm. ; nil.
+1920	Kent, Otford	P. Harwood	?	Hope Museum, Oxford ; nil.
+1921	Kent, Westerham	P. Harwood	?	Hope Museum, Oxford ; nil.
+1921	Herts., Watford	N. Joy	B	Joy (1921).
+1921	Surrey, Ranmore	A. M. Massee	?	pers. comm. ; nil.
+1923	Surrey, Boxhill	A. M. Massee	?	pers. comm. ; nil.
+1924	Herts., Bricket Wood Scrubs	P. Harwood	?	Liverpool Museum ; nil.
+1925	Berks., Windsor Forest	H. Donisthorpe	*P.b.*, *T.g.*, *G.a.*	Donisthorpe (1939).
+1926	Kent, Cobham Park	A. M. Massee	*P* on birch and hornbeam	pers. comm. ; nil.
1926	Surrey, Ashtead Common	H. Donisthorpe	?	pers. comm. from J. L. Henderson ; ? nil.
1926	Surrey, Oxshott Common	O. W. Richards	*P.b.*	Richards (1926).
1931	Kent, Beckenham	S. R. Ashby	?	pers. comm. from J.L. Henderson ; nil.
1931	? Kent, Bromley	Mr. Jacobs	?	[Jacobs] (1931).
1933	Kent, Swanley Wood, Farningham	A. A. Allen	F " in boleti "	Allen (1935).
+1933	Sussex, Arundel	A. A. Allen	B of beech	Allen (1935).
1935	Surrey, Woking	J. J. Walker	?	Hope Museum, Oxford ; nil.
+1936	Oxon, Watlington	E. W. Jones	?	Hope Museum, Oxford Manchester Museum, Salzman (1939).
1938	Kent, Eynsford	F. D. Buck	*P*	pers. comm. ; nil.
+1938	Notts., Sherwood Forest	Mrs. H. Burleigh	*P.b.*	Hudson Beare (1939).
+1941–43	Hants-Surrey, S.E. of Mychett Lake	E. A. J. Duffey	*P*	Duffey (1945).
+1942	Cheshire, Pexhill, nr. Macclesfield	G. C. and G. W. R. Bartindale	?	Bartindale and Bartindale (1948).
+1943	Cheshire, Thorneycroft Pool, Siddington	F. J. Kinsey	*P.b.*	Manchester Museum ; Tindall (1943).
1944	Beds., Sewell, Houghton Regis, Dunstable	E. Milne-Redhead	B	Airy Shaw (1945).
1944	Beds., Sundon, nr. Luton	E. Milne-Redhead	B	Airy Shaw (1945).
1944	Beds., N.W. of Houghton Regis	E. Milne-Redhead	F	Airy Shaw (1945).
1944	Beds., Heath and Reach	E. Milne-Redhead	*P.b.*	Airy Shaw (1945).
1944	Bucks., " Soulsby " [? Soulbury, S. of Shire Oak]	E. Milne-Redhead	*P.b.*	Airy Shaw (1945).
1944	Beds., Milton Bryan	E. Milne-Redhead	*P.b.*	Airy Shaw (1945).
1946	Beds., Luton Hoo	B. Verdcourt	B	Verdcourt (1952).

Year	County and locality	Collector	Habitats	Source of information
+1947	Cheshire, Tatton	H. Britten	*T.g.*	Manchester Museum ; nil.
+1949	Cambs., Wicken Sedge Fen and Chippenham Fen	A. M. Massee	?	Massee (1949).
+1949	Cheshire, Cotterill Clough, nr. Ringway Aerodrome	H. Britten	*F.a.*	Manchester Museum ; nil.
+1949	Sussex, Groombridge	F. D. Buck	F on birch (? *P.b.*)	pers. comm. ; nil.
+1950	Hants, Matley Bog (between Lyndhurst and Beaulieu)	W. D. Hincks	?	pers. comm. ; Manchester Museum ; nil.
+1950	Cheshire, Nether Alderley, nr. Macclesfield	G. C. Bartindale	Sweeping	pers. comm. ; nil.
1951	Cheshire, West Park, Macclesfield	G. W. R. Bartindale	F on beech	pers. comm. ; nil.
1952	Kent, Knole Park, Sevenoaks	A. A. Allen	F	Allen (1952).
+1953	Berks., Wytham Woods	C. Elton	*P.b.*, ? *P.a.*, B	Bureau of Animal Population records, Oxford ; nil.
[1955–59]	Berks., Wytham Woods	K.P.S.	*P.b.*, *P.a.*, *P.sq.*, *P.s.*, *I*, *G.a.*, *Pst.h.*	Bureau of Animal Population records, Oxford ; nil.
1955	Epping Forest	F. D. Buck	*P*	Buck (1955).
1956	Hunts., Holme Fen	*	*P.b.*	B.A.P. records ; nil.
1956	Hunts., Monks Wood	*	*P.b.*	B.A.P. records ; nil.
+1956	Sussex, Old Park Wood, nr. Chichester	*	*P.b.*	B.A.P. records ; nil.
1956	Hants, Borden Wood, nr. Liss	*	*P.b.*	B.A.P. records ; nil.
+1956	Wilts., Savernake	*	*P.b.*	B.A.P. records ; nil.
+1956	Suffolk, nr. Chillesford	*	*P.b.*	B.A.P. records ; nil.
+1956	Hants, nr. Brockenhurst	*	*P.b.*	B.A.P. records ; nil.
1957	Surrey, Wimbledon Common	*	*P.b.*	B.A.P. records ; nil.
1957	London, Putney Heath	*	*P.b.*	B.A.P. records ; nil.
1957	Berks., Cothill Fen	*	*P.b.*, *P.a.*	B.A.P. records ; nil.
1957	Notts., nr. Ollerton	*	*P.b.*	B.A.P. records ; nil.
1957	Hants, Tantany Wood, Penerly, nr. Beaulieu	*	*P.b.*	B.A.P. records ; nil.
+1957	Dorset, nr. Wareham	*	*P.b.*	B.A.P. records ; nil.
+1957	Wilts., Grovely Wood, nr. Gt. Wishford	*	*P.b.*	B.A.P. records ; nil.
+1957	Lincs., nr. Market Rasen	*	*P.b.*	B.A.P. records ; nil.
+1957	Gloucs., Westonbirt	*	*P.b.*	B.A.P. records ; nil.
+1957	Dorset, Morden Heath	*	*P.b.*	B.A.P. records ; nil.
+1957	Dorset, Wimborne St. Giles	*	*P.b.*	B.A.P. records ; nil.
+1957	Dorset, Arne Big Wood	*	*P.b.*	B.A.P. records ; nil.
1957	Leics., Swithland Wood	*	*P.b.*	B.A.P. records ; nil.
1957	Norfolk, nr. Thetford	*	*P.b.*	B.A.P. records ; nil.
1957	Suffolk, Barton Mills	*	*P.b.*	B.A.P. records ; nil.
1957	Norfolk, nr. Swaffham	*	*P.b.*	B.A.P. records ; nil.
1957	Lincs., halfway between Lincoln and Newark	*	*P.b.*	B.A.P. records ; nil.
1957	Berks., nr. Risely	*	*P.b.*	B.A.P. records ; nil.
1957	Surrey, Black Down	*	*P.b.*	B.A.P. records ; nil.
1957	Hants, nr. Fleet	*	*P.b.*	B.A.P. records ; nil.
1958	Kent, Shorne	K. C. Side	*Pst.*	pers. comm. ; nil.
+1958	Norfolk, Calthorpe Broad	*	*P.b.*	B.A.P. records ; nil.
+1958	Kent, Treneleypark Wood, Fordwich	K. C. Side	*P* on birch	pers. comm. ; nil.

Year	County and locality	Collector	Habitats	Source of information
1958	Kent, Darenth Wood, nr. Dartford	K. C. Side	*P.* on birch	pers. comm. ; nil.
1958	Sussex, Balcombe Forest, nr. Handcross	K. C. Side	F	pers. comm. ; nil.
1958	Sussex, St. Leonard's Forest, nr. Horsham	K. C. Side	F	pers. comm. ; nil.
1958	Berks., nr. Pangbourne	*	*P.b.*	B.A.P. records ; nil.
+1958	E. Sussex, Possingworth Park, Cross-in-Hand	E. Lewis	B	pers. comm. ; nil.
1958	Kent, Bitchett Common, nr. Sevenoaks	K. C. Side	F	pers. comm. ; nil.
1958	Sussex, Ashdown Forest, nr. Uckfield	*	*P.b.*	B.A.P. records ; nil.
1958	Hants, Brockenhurst	J. L. Henderson	*G.a.*	pers. comm. ; nil.
+1958	E. Suffolk, Aldeburgh	E. Lewis	*P.sq.*	pers. comm. ; nil.
+1958	Norfolk, nr. Castle Rising	*	*P.b.*	B.A.P. records ; nil.
+1959	Yorks., Skipworth Common, about halfway between York and Selby	*	*P.b.*	B.A.P. records ; nil.
+1959	Glamorgan, nr. Felindre	*	*P.b.*	B.A.P. records ; nil.
+1959	Isle of Wight, Osborne Forest	*	*P.b.*	B.A.P. records ; nil.

APPENDIX II

List of localities from which *Cis bilamellatus* appears still to be absent. (In brackets after each locality is given the number of dead old *Polyporus betulinus* fruiting-bodies examined by the author while looking specifically for *Cis bilamellatus*.)

By counties from south to north: DEVON: Yarner Wood, nr. Exeter (17); GLOUCESTERSHIRE: Forest of Dean (3); Ford, nr. Temple Guiting (6); WORCESTERSHIRE: Storridge, nr. Gt. Malvern (3); Wyre Forest, nr. Bewdley (3); CAERNARVONSHIRE: Beddgelert (3); YORKSHIRE: nr. Kilburn (1); Yearsley Moor (1); NORTH LANCASHIRE: Deanholme Wood, nr. Haverthwaite (3); Low Wood, nr. Haverthwaite (2); WESTMORLAND: Borrow Beck, nr. Tebay (1); nr. confluence of R. Eamont and R. Eden (16); CUMBERLAND: Ullswater (2); DURHAM: nr. Durham (8); NORTHUMBERLAND: Riding Mill (2); nr. Alnwick (2); MIDLOTHIAN: nr. Edinburgh (9); FIFE: nr. Morton Lochs, Tents Moor (1); DUNBARTON: three sites along Loch Lomond (10); PERTHSHIRE: Lochearnhead (2); Loch Tummel (5); three main sites along Loch Rannoch (7); ANGUS: two sites in Glen Esk (12); Loch Lee (3); Glen Mark (2); KINCARDINE: nr. Banchory (3); ABERDEENSHIRE: between Braemar and Balmoral (1); Glen Quoich, Mar Forest (1); New Deer (5); INVERNESS-SHIRE: Rhum (3); Fort William (2); Aviemore (2); Inchriach (1); BANFFSHIRE: Troup Head (3).

POSTSCRIPT

27th September, 1960.

1. Since this manuscript went to press a note by J. J. Walker, which was not indexed in the *Ent. mon. Mag.*, has been brought to my notice.

> (Walker, J. J., 1935, New localities for *Cis bilamellatus* Wood. *Ent. mon. Mag.* **71** : 245.) This calls for two alterations in Appendix I. The records for Wytham Woods, Berks., at the end of the 1944–53 ten-year interval, have been antedated and should instead begin the 1934–43 interval:

Year	County and locality	Collector	Habitats	Source of information
" 1935	Berks., Wytham Woods	J. Collins	*P.b.*	Walker (1935)."

and the Woking, Surrey, record, which now follows it, should read :

" 1935	Surrey, Woking	J. J. Walker	*P* on lime	Hope Museum, Oxford ; Walker (1935)."

2. Additional localities in which *Cis bilamellatus* has been found are :

Year	County and locality	Collector	Habitats	Source of information
1959	Surrey, Tilburston Hill, Godstone	E. Lewis	B of beech	pers. comm. ; nil.
1960	Yorks., Askham Bog, *c.* 3 miles S.W. of York	*	*P.b.*	B.A.P. records ; nil.

3. Additional localities from which *Cis bilamellatus* is still absent :

WORCESTERSHIRE : Wyre Forest (1 more fruiting-body of *Polyporus betulinus* examined) ; MONTGOMERYSHIRE : nr. Welshpool (5 on 1 tree) ; CAERNARVONSHIRE : Aber Falls (24 on 3 trees) ; YORKSHIRE, WEST RIDING : Wharfedale : nr. Yockenthwaite (3 on 1 tree) ; Strans Wood, nr. Yockenthwaite (2 on 2 trees) ; nr. Litton (8 on 3 trees) ; nr. Arncliffe (3 on 2 trees) ; nr. Burnsall (1) ; NORTH RIDING : Hundred Acre Wood, halfway between Sutton on the Forest and Strensall, *c.* 6½ miles N. of York (2 on 1 tree) ; Sutton on the Forest, *c.* 7½ miles N. of York (2 on 2 trees) ; Yearsley Moor (7 more on 6 trees) ; *c.* 3 miles S. of Thirsk (1) ; nr. Dalton upon Tees, *c.* 4 miles S. of Darlington (5 on 4 trees) ; nr. Croft, *c.* 3 miles S. of Darlington (examined 1 collection of dead *Polyporus adustus* containing Ciidae, on wych elm) ; DURHAM : " Nanny's Plantation ", between Wingate and Wheatley Hill, almost E. of Durham (10 on 6 trees).

4. In Wales, therefore, another large collection indicates that *Cis bilamellatus* has not yet reached the N.W. corner, though it is present in the south. There is still too little information for central Wales and the W. Midlands of England for its distribution there to be mapped.

For northern England, the extensive collections recorded above show that it seems not yet to have spread north of York, nor has it yet appeared in Wharfedale in the West Riding of Yorkshire. I have found that the region north of York has plenty of birch with *Polyporus betulinus*, so that the beetle's absence from this part can scarcely be due to lack of suitable habitat.

OBSERVATIONS ON THE SALINITY TOLERANCE AND HABITS OF A EURYHALINE CADDIS LARVA, *LIMNEPHILUS AFFINIS* CURTIS (TRICHOPTERA : LIMNEPHILIDAE)

By D. W. Sutcliffe

(Dept. of Zoology, University of Durham, King's College, Newcastle-upon-Tyne)

I. Introduction

At the turn of this century Silfvenius (1906) investigated the distribution of caddis larvae in the Gulf of Finland. He found 39 species, representing several families of the Trichoptera, in water of less than 2‰ salinity. As the salinity increased in the western region of the Gulf so the number of species gradually diminished, but Silfvenius found 19 species, including *Limnephilus affinis* Curtis, in the highest salinities recorded, 5–6‰. This species is widely distributed throughout Europe and is particularly common in Holland, Belgium, the north of France and in Britain (McLachlan, 1874–80). It has been found both in fresh-water and brackish-water habitats (Marlier, 1949). McLachlan (*loc. cit.*, p. 82) states that the adult is extremely common in Britain from April to October, mostly frequenting woods, but very varied in its habits. On one occasion he found the adults in abundance " on a wide barren expanse on the sea shore, hiding among the scanty herbage round shallow pools which must frequently have received sea water during storms and high tides ". Although *L. affinis* and several other species found by Silfvenius in the Gulf of Finland are generally recognised as euryhaline species (*e.g.* Despax, 1951), little is known concerning the range of salinities which these caddis are able to tolerate.

The presence of a large population of *L. affinis* in a salt-marsh at Seaton Sluice, Northumberland, provided an opportunity to examine the salinity tolerance of this caddis. Parts of the salt-marsh are inundated by sea water at least once a month during the autumn and winter, and this results in considerable fluctuations of the salinity. Investigations on the survival of the caddis in water of varying salinity, both in the salt-marsh and in the laboratory, are presented in this paper, and the habits of the larva are described. Osmotic and ionic regulation in the larva was also investigated and compared with regulation in several species of caddis obtained from fresh-water habitats ; the results of this work will be published elsewhere.

II. The Salt-marsh

The salt-marsh is situated at the head of an estuarine mud-flat which is regularly inundated with sea water, but only the highest spring tides reach the salt-marsh proper. The latter is an area of rough ground, an acre in extent, which is intersected by a regular series of shallow pools. The bottom of the pools consists of thick mud, and most of them contain a layer of decaying leaves which are blown on to the salt-marsh from neighbouring trees. There is no permanent vegetation in the pools but an abundant growth of *Chaetomorpha*, a green filamentous alga, appears during the autumn.

In addition to *L. affinis* several other insects were found in the salt-marsh during the period September to May. Larvae of *Chironomus aprilinus* Meigen were very common throughout the winter. Larvae of *Ephydra riparia* Fallén were found each year during September and October, and the larval and pupal stages of *Aëdes detritus* Edwards occurred during periods of mild weather. Larvae of *Colymbetes fuscus* L. were occasionally seen during the autumn. All these insects were able to survive short periods of immersion in sea water with a salinity of 33‰. The remaining fauna

consisted of *Sphaeroma rugicauda*, *Corophium volutator* and *Gammarus duebeni*, all of which are typical brackish-water crustaceans. Many of the pools also contained specimens of the three-spined stickleback, *Gasterosteus aculeatus*.

Salinity Fluctuations

Regular determinations of the salinity in selected pools were obtained over a period of more than two years. The pools are divisible into two groups, North and South, and the fluctuations in salinity differed in these groups during the period September to March. In the North pools, which are nearest to the tidal mud-flat, it fluctuated mainly between 20‰ and 30‰ and rarely fell below 15‰. The South pools are situated on slightly higher ground ; the salinity rarely exceeded 15‰, and was often not more than 10‰ for several consecutive weeks.

The North pools were affected by the highest spring tides in every month from September to May, but the South pools, particularly several lying on the highest part of the salt-marsh, were inundated with sea water only during the spring tides of the September and March equinoxes. These tides raised the salinity to 25‰ in the South pools and 32–33‰ in the North pools. Since the pools are very shallow subsequent rainfall lowered the salinity by approximately 10‰ within seven days following a high tide. Further details of the salinity fluctuations will be published elsewhere.

From May until August the pools were impermanent and they contained water only during periods of heavy rainfall or abnormal tides. In May or early June, in 1956–59, the entire salt-marsh dried up and the population of caddis in the pools was destroyed.

III. Salinity Tolerance of the Caddis

Larvae of *L. affinis* were kept in different concentrations of local sea water diluted with Newcastle tap water. In the following account the dilutions are expressed as a percentage of sea water, which has a salinity of approximately 35‰, and the actual salinities are given in brackets.

The larvae lived for several months in concentrations varying from 0 to 75 per cent. sea water (26‰ salinity) at temperatures between 5 and 15° C., and in 0 to 60 per cent. sea water (21‰) at room temperature (18–22° C.). In 75 per cent. sea water at room temperature the larvae survived for 2–4 weeks. In concentrations approaching that of normal sea water the majority of the larvae survived for only a few days, but some individuals lived for more than a week in approximately 85 per cent. sea water (30‰) at 15° C.

The ability of the caddis to emerge as imagines from concentrations of sea water similar to those found in the salt-marsh was examined in the laboratory. Sixty medium-sized larvae were taken from various South pools on 11th November, 1957, and divided into six groups of ten larvae. Three groups were placed in tanks containing 25, 50 and 75 per cent. sea water (8·5, 17 and 26‰) respectively. These tanks were maintained at room temperature, which fluctuated mainly between 14° and 18° C. during the experiment. The remaining three groups were also placed in 25, 50 and 75 per cent. sea water, but the tanks were maintained at 6–9° C. in a large water bath cooled by a refrigerator unit. Sand and gravel was placed in the bottom of the tanks and the larvae were regularly supplied with dead sycamore leaves and occasionally with *Chaetomorpha*.

The results of the experiment are presented in Table I. All the larvae in 75 per cent. sea water at room temperature died within 14 days, although in other experiments some larvae have survived for more than three weeks at room temperature.

Eight to nine weeks after commencing the experiment two adults had emerged from 25 per cent. sea water and three from 50 per cent. sea water at room temperature. During the next six weeks several more adults emerged, and of the seven

TABLE I.—*The effects of salinity and temperature on the survival of* L. affinis *Curtis*

Concentration of sea water (actual salinity in parenthesis)	Temperature (°C.)	Time in weeks after start of experiment							
		2	4	8	9	10	11	.....	15
25% (8·5‰)	14–18	9*l*, 1*dl*	6*l*, 1*dl*	1*l*	1*l*	1*l*	1*l*		1*l*
			2*p*	6*p*	5*p*	3*p*	3*p*		1*dp*
				1*A*	1*A*	2*A*	.		2*A*
	6–9	10*l*	9*l*, 1*dl*	9*l*	6*l*	6*l*	6*l*	Maintained at 14–18° C. after 11th week	4*l*, 1*dl*
					3*p*	3*p*	3*p*		1*p*
									3*A*
50% (17‰)	14–18	10*l*	7*l*, 1*dl*	3*l*	1*l*, 1*dl*	1*l*	1*l*		1*l*
			2*p*	4*p*	4*p*	4*p*	4*p*		.
				2*A*	1*A*	.	.		4*A*
	6–9	10*l*	9*l*	9*l*	9*l*	9*l*	8*l*	Maintained at 14–18° C. after 11th week	6*l*
			1*p*	1*p*	1*p*	1*p*	2*p*		2*p*
									2*A*
75% (26‰)	14–18	All dead							
	6–9	10*l*	9*l*, 1*dl*	7*l*, 2*dl*	7*l*	7*l*	6*l*, 1*dl*	Maintained at 9–10° C. after 11th week	3*l*, 2*dl*
									1*dp*

Abbreviations: *l*, larva; *dl*, dead larva; *p*, pupa; *dp*, dead pupa; *A*, adult.
All adults, dead larvae and dead pupae were removed from the tanks when found.
Note.—Those larvae which were found dead in the tanks of 25 per cent. and 50 per cent. sea water had been killed and eaten by the other larvae.

larvae which pupated in 25 per cent. sea water only one failed to emerge. In 50 per cent. sea water all seven of the larvae that pupated had successfully emerged. It will also be noticed that adults emerged from those larvae that had pupated in 25 per cent. and 50 per cent. sea water at 6–9° C. when the tanks were later kept at room temperature. No larvae pupated during the first 11 weeks in 75 per cent. sea water at 6–9° C. Furthermore, the larvae were very inactive and did not feed. In other experiments using concentrations greater than 60 per cent. sea water the larvae also became very sluggish in their movements, and the majority did not feed.

The experiment clearly demonstrates that *L. affinis* is able to complete its life-cycle in 50 per cent. sea water. Imagines have not been reared from 75 per cent. sea water, which is the highest concentration in which the larvae will survive for several weeks. The experiment also demonstrates the effect of temperature on the rate of both larval and pupal development. In 25 and 50 per cent. sea water, maintained at room temperature throughout the experiment, the larvae matured rapidly and the pupal stage occupied approximately four weeks, but at 6–9° C. the majority of the larvae did not pupate during 11 weeks and the single pupa in 50 per cent. sea water did not emerge during seven weeks. When the temperature was raised to 14–18° C. for four weeks the pupae rapidly emerged, but six larvae in 50 per cent. sea water had still not matured. The effect of low temperature on the larval stage appears to be a reduction in the general activities of the larva. Only one larva pupated in 75 per cent. sea water during 15 weeks at 6–9° C., and this pupa was dead when examined. The remaining three larvae were placed at room temperature after the fifteenth week and they died within seven days.

IV. Habits of the Larva

Eclosion

No egg-masses were found in the pools at Seaton Sluice and it is probable that, as in other genera of the Limnephilidae, they are deposited amongst the surrounding vegetation (Lestage *in* Rousseau, 1921; Flint, 1956). On 19th September, 1957, at 2.30 p.m., large numbers of tiny, caseless larvae were found clinging to grass stems

overhanging several of the South pools, and larvae were also floating on the surface film. They were observed to penetrate the surface film by climbing down the partly submerged grass stems, " wetting " the cuticle in the process. On this particular day the weather was fine and warm but the preceding three days had been very wet, and the ground was damp and " steaming " in the afternoon sunshine.

A few larvae were found in the pools during the last two weeks in August but, in the summers of 1956–58, the peak period of emergence occurred in the second and third weeks of September. During these two weeks the caseless larvae were extremely common and were observed crawling amongst the filaments of *Chaetomorpha*, with which they built a temporary case ; this was rapidly replaced by a case built with dead leaves and/or mineral materials. It is interesting to note that the peak period of eclosion coincided with the very high spring tides of the autumn equinox. At this time the salt-marsh is very wet underfoot and eclosion probably occurs only in moist or very humid conditions.

General Remarks

Larvae were most abundant in the South pools, where the salinity was normally below 15‰, but considerable numbers were present in all the pools, including several shallow pools on the extreme edge of the tidal mud-flat. No quantitative analysis of the population was undertaken but the presence of fully-grown larvae by the end of November suggests that a small proportion developed rapidly during the autumn. Some of these large larvae were brought into the laboratory and kept at room temperature during the winter months. They pupated during December and January, and the imagines emerged in the last week of February. No pupae were found in the salt-marsh before March, when the water temperature rose above 10° C., having fluctuated between 8° and 0° C. since November. During very severe weather the pools were frozen nearly solid. At temperatures lower than 6° C. the activity of the larvae decreased considerably ; many had withdrawn into their cases and were completely inactive. During the winter several of the shallowest pools periodically contained no water for as long as five days. The larvae were found grouped together under leaves and many were half-buried in the moist mud. Practically all the larvae survived these short periods of desiccation. At the end of April, in 1956–59, the South pools began to dry up and the larvae were exposed for several days at a time ; on one occasion larvae survived temperatures of 22–24° C. on the dry surface of the mud. Subsequent rainfall filled the pools two to three days later and the larvae were still very active. In May the entire salt-marsh eventually dried up, and the caddis population was annihilated. Most of the larvae were only approximately 10 mm. in length and only a few pupal cases were found amongst hundreds of larval cases which were examined. When the caddis population is destroyed the salt-marsh is probably re-colonised by adults of *L. affinis* which emerge from Seaton Burn during the late summer months. The caddis occurs in the burn above the estuarine region but only a few larvae have been found in the estuary itself.

Food

In the salt-marsh pools the larvae fed mainly on dead leaves of sycamore and elm, blown in from a nearby copse, which also contains beech and birch trees. The larvae were unable to feed on the leaves of these latter until they began to decay in the following spring. Apart from the sporadic appearance of *Chaetomorpha*, a brackish-water alga, during the autumn, no other vegetation was available and the caddis population appears to be dependent on the annual leaf-fall from the neighbouring trees.

Hanna (1957) has recently investigated the growth and feeding habits of *Limnephilus politus* McLachlan and *L. marmoratus* Curtis, and decided that these

species are essentially detritus feeders, although they may also utilise unicellular organisms, algae and dead leaves, all of which were found in the gut contents. Satija (1957) noted that the larvae of *L. stigma* Curtis fed on dead as well as fresh plant material. Lloyd (1915) examined the gut contents of two American species, *L. combinatus* and *L. indivisus* ; these fed on dead and decaying vegetable material (cat-tail, sedges, *etc.*) as well as on living plant tissue, apparently with little discrimination. These observations indicate that dead leaves form at least a regular part of the diet of these species of *Limnephilus*. It was, therefore, of considerable interest to find that *L. affinis* could be reared solely on a diet of dead leaves. Leaves were periodically collected from the salt-marsh and sometimes stored in polythene bags for several weeks before being given to the larvae. No epiphytic organisms were found on the surfaces. Larvae of *L. stigma* were also reared on a diet of these leaves.

The larvae of *L. affinis* are not exclusively herbivorous. Observations in the laboratory showed that the caddis will readily attack and consume the larvae of *Chironomus aprilinus* Meigen and *Ephydra riparia* Fallén, both of which were found in the salt-marsh pools. Furthermore, on several occasions larvae in the salt-marsh were observed feeding on the decaying bodies of the three-spined stickleback, *Gasterosteus aculeatus*. The larvae also display a strong tendency to devour one another, particularly when several are confined together in a small tank. Cannibalism occurs even when they are amply provided with vegetable material. The method of attack followed the same general pattern in a number of observed instances, and empty larval skins found in laboratory stocks of the caddis showed signs of similar treatment. When two larvae came into contact they reared up in the water and struck out with all three pairs of legs, each seeking to gain a hold on the anterior abdominal segments of the other. In a successful attack the victor seized the larva from below and gripped the second–third abdominal segments with its second and third pair of legs, which were wrapped completely round the struggling larva. A small piece of cuticle was then torn with the mandibles from the ventral surface of the first or second abdominal segments, which were unprotected by the case. The tissues of the thorax were then consumed by thrusting the head through the abdominal opening. The dying larva was pulled out of its case during this process and the attacker then enlarged the ventral opening towards the posterior end of the abdomen, eating the entire abdominal contents as it did so. The contents of a larva were consumed in less than two hours, leaving only the cuticle, legs and head untouched. Attacks directed at the dorsal surface were invariably unsuccessful since the attacked larva immediately withdrew into its case.

There are a number of records of animal remains in the gut contents of herbivorous caddis larvae, including the remains of other caddis larvae, and many species are apparently omnivorous (Slack, 1936). During the present investigation it was confirmed that the larvae of *Limnephilus stigma* and *Anabolia nervosa* Leach will readily devour Chironomid larvae.

V. Discussion

In addition to *L. affinis*, at least one other species of caddis is able to tolerate high salinities. Hutton discovered the larvae of *Philanisus plebeius* Walker in the rock pools of Lyttleton Harbour, New Zealand (McLachlan, 1882). The rock pools were situated between high and low watermark and the caddis was later found in similar situations elsewhere in New Zealand and in Australia. Hutton was able to keep the caddis alive for several months in jars of sea water, although only one imago emerged. The life-history and habits of this marine caddis were described by Hudson (1904). Hagen (1883) found a single unidentified " phryganid " larva on wharf piles in a rock-pond connected with the sea, but it is not known certainly whether this caddis was truly marine. Other records of Trichoptera in brackish water are all of caddis larvae found in water of less than 9‰ salinity, and other orders of Insects

show a similar relation to salinity. Thus, although a considerable number of insects, representing all of the major groups that are normally found in fresh water, have been found occasionally in slightly brackish water, particularly in the Baltic Sea, a study of several faunal lists, including those given by Johnsen (1946), Lindberg (1948), Butler and Popham (1958), shows that only certain Hemiptera, Coleoptera and Diptera occur in salinities greater than 10‰.

The effects of an influx of highly saline water on an established low-salinity fauna have been described recently by Butler and Popham (1958). No Ephemeroptera or Trichoptera were found in water more saline than 25 per cent. sea water, and most of the Odonata, Hemiptera and Coleoptera were also absent. Butler and Popham suggested that this salinity is critical to many fresh-water insects, and the investigations of other workers support this view. In the salt-marsh at Seaton Sluice it was noted that several species of Hemiptera and Coleoptera migrated from the pools whenever the salinity exceeded approximately 10‰. Studies of osmotic and ionic regulation in larvae of *Aëdes aegypti* (L.) and *Culex pipiens* L. (Wigglesworth, 1938) and *Sialis lutaria* L. (Shaw, 1955) indicate that salt concentrations equivalent to 30–40 per cent. sea water (10–14‰ salinity) represent the limit of tolerance in these insects and this is supported by the similarity of the results obtained by the writer with several species of fresh-water caddis larvae, including *Limnephilus stigma* and *Anabolia nervosa*.

In contrast, the larvae of *L. affinis* are able to live for several months in water of 26‰ and survive for several days in salinities approaching that of normal sea water. In the majority of the pools at Seaton Sluice salinities greater than 26‰ occurred only during very high spring tides, after which the salinity decreased rapidly within a few days. In the South pools, where the caddis is particularly abundant, the salinity was considerably less than 26‰. Hence *L. affinis* is well adapted to survive the salinity changes which occur naturally in the salt-marsh, and the habitat is very suitable for it ; considerably more than one thousand larvae occur in each of the South pools, which are about 30 feet long and 2–3 feet wide. The salt-marsh has been populated for more than thirty years (Dr. H. O. Bull, *personal communication*) by the caddis, which has not been found in any of the other salt-marshes and estuaries in Northumberland.

VI. Summary

A large population of *Limnephilus affinis* Curtis has been found in a salt-marsh where the salinity fluctuated between 1‰ and 33‰. The larvae survive for several months in 26‰ salinity at temperatures below 15° C., and for short periods of immersion in approximately 30‰ salinity. The caddis is able to complete its life-cycle in approximately 17‰ salinity, and has been reared on a diet of dead sycamore and elm leaves. It is well adapted to survive the salinity changes which occur in the salt-marsh and has colonised the habitat for more than 30 years.

VII. Acknowledgments

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Book Notice

Introduction to Entomology. By R. Jeannel. Translated by Harold Oldroyd. 8vo. London (Hutchinson), 1960. Pp. 344 : text illust. £3 3*s*.

The usual text-book approach to entomology is not followed in this work which, instead, presents the subject on a broader and more comparative basis, dealing with it in three main sections.

In the first section on Anatomy and Classification the origin of insects, their external morphology, internal anatomy, development and the basis of their classification are dealt with. The second section on biology covers their physiology, behaviour and social life.

The third section on palaeontology and geographical distribution describes the evolution of insects, with illustrations of many fossil species. This section includes a chapter on the spread of insects and their vicissitudes during their colonisation of the earth, based on the fossils from all the geological periods, and ends with an account of the natural regions of the world as now defined.

The numerous illustrations are mainly of living insects, of which forty-six species are displayed in colour and there are many detailed anatomical and physiological diagrams.

A general index completes the volume.

PROPRIOCEPTIVE SETAE IN THE NECK OF THE COMMON EARWIG (*FORFICULA AURICULARIA* L.)

By Edward J. Popham

(*Department of Zoology, The University of Manchester*)

Introduction

Goodman (1959) and Haskell (1959) have described a group of tactile setae situated on the front end of each anterior lateral cervical sclerite of *Locusta migratoria* L. These setae, and others on the anterior pronotal edge, are proprioceptors for perceiving head movements. *Locusta* and related insects feed at the leaf edge and the mouthparts are so designed that they function effectively only when the head is lowered (Popham, 1959*a* and *b*). In these insects lateral head movements are restricted by the anterior thoracic margins and occur mainly in the sagittal plane. In association with these feeding habits, the neck of *Locusta* is covered with arthrodial membrane, laterally strengthened by the two pairs of lateral cervical sclerites, which form a lever system for moving the head relative to the thorax. The absence of ventral cervical sclerites in these Orthoptera is associated with the fact that the neck has no need for support ventrally.

In contrast, the Cricket (*Gryllulus domesticus* L.) and the Cockroach (*Periplaneta americana* L.) feed when the head is held in any position, whereas the Common Earwig (*Forficula auricularia* L.) can feed only when the head is raised (Popham, *l.c.*). These feeding habits are associated with differences in the cervical structure, that of the earwig being the most complex. *Forficula auricularia* lives in a variety of habitats, such as litter, under bark, and in compressed vegetable matter. The earwig neck can be made flexible or rigid as circumstances require. A study of the distribution of the proprioceptive setae in the earwig neck is, therefore, of interest.

Techniques

The movements of the head and neck have been studied in living insects. The structure of the neck was investigated in material prepared as follows. The anterior end of the insects was fixed in either Bouin or Carnoy's fluid. Some were then embedded in celloidin and thick sections cut and stained with haematoxylin. The remainder of the material was dehydrated, placed in methylbenzoate for a week and then in 1 per cent. celloidin in methylbenzoate for a similar time before being embedded in paraffin wax, serially sectioned at 10 μ and stained with either haematoxylin and eosin or by Masson's technique.

Neck of *Forficula auricularia*

As a detailed account of the functional morphology of the earwig neck is given elsewhere (Popham, 1959*b*), it is sufficient to summarise the main features and explain its form and function. The neck of *Forficula auricularia* is in the form of a short cylinder with dorsally inclined oblique ends. The wide range of head movement is associated with a reduction of the lateral cervical sclerites and their function is performed by a collar-like structure, which may be described as follows. On the dorsal side of the neck, immediately behind the capsule, are two transverse folds (fig. 4 *ATF*, *PTF*) in the arthrodial membrane. Laterally, these folds run downwards and backwards to the lateral margins of the prothoracic sternum, the anterior fold running lateral to the lateral sclerites, while the posterior fold is mainly confined to

the dorsal side of the neck and appears laterally as a shallow groove anterior to the lateral plates (*LP*). In *Forficula*, the anterior fold forms a collar-like structure and the arthrodial membrane is raised into numerous flat domes, which permit folding to take place in any direction. If the two sides of a fold are in close contact, the domes on each side form an interlocking mechanism, making the neck rigid, when inflated by haemocoelic fluid pressure. By this means the head can be held in any position while feeding. Ventrally, the neck is supported by two ventral cervical sclerites (*AVCS* and *PVCS*), the anterior being the smaller. The arthrodial membrane is invaginated under the anterior margins of the two sclerites as well as under the front of the prosternum (*PS*). The ventral arthrodial membrane is raised into a series of transverse ridges, which allow the membrane to be rolled only in the transverse plane. Between the anterior ventral and posterior lateral cervical sclerites (*LCS*) are a pair of latero-ventral sclerites (*LVS*), situated one on each side of the neck. Dorsally the neck bears a median dorsal sclerite situated between the head and anterior cervical fold and a pair of latero-dorsal sclerites (*LDS*) between the two folds of the neck.

Distribution of Setae

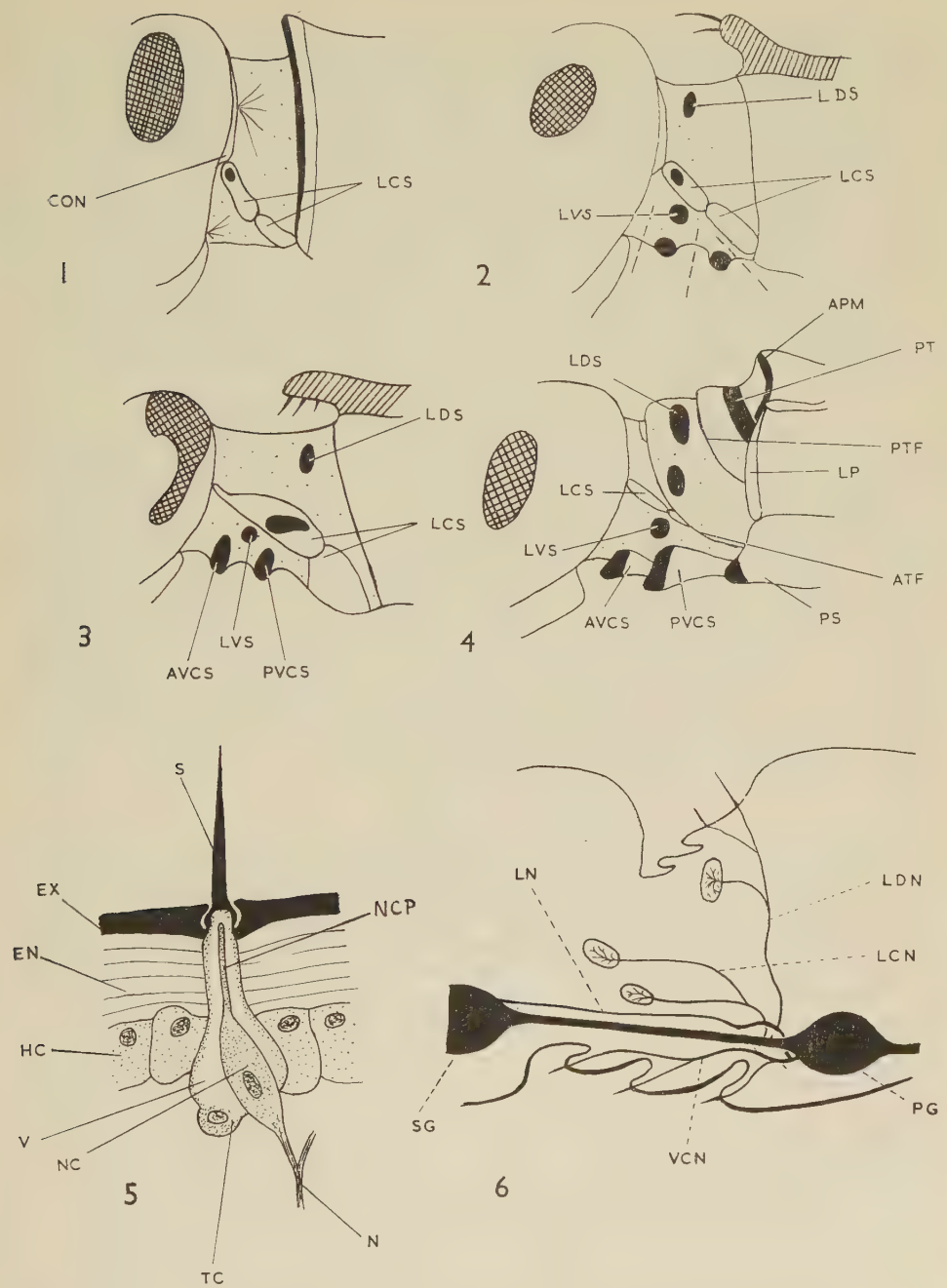
Groups of tactile setae are distributed on the surface of the earwig neck on the latero-dorsal sclerites, pretergum, anterior pronotal margin (*APM*), the anterior cervical fold, the latero-ventral sclerites and the anterior margins of the ventral cervical sclerites and prosternum. The setae of the anterior cervical fold are arranged in a vertical row, while those on the pretergum and pronotum are more sparsely distributed than on other sclerites.

Form of Setae (fig. 5)

The setae are straight or slightly curved, arising from a small dome-like base, situated in a shallow hemispherical depression in the outer region of the exocuticle (*EX*). The setae are hollow and contain a fine process arising from a vacuolated trichogenous cell (*TC*) in the hypodermis. The nerve cell process (*NCP*) to each seta is situated centrally and the seta is free to bend in any direction, returning to its initial position by virtue of the elasticity of the cuticle.

Explanation of Figure Lettering

APM, Anterior pronotal margin
ATF, anterior transverse cervical fold
AVCS, anterior ventral cervical sclerite
CON, occipital condyle
EN, endocuticle
EX, exocuticle
HC, hypodermal cell
LCN, lateral cervical nerve
LCS, lateral cervical sclerites
LDN, latero-dorsal cervical nerve
LDS, latero-dorsal cervical sclerite
LN, lateral cervical nerve
LP, lateral plate
LVS, latero-ventral cervical sclerite
N, nerve fibres from nerve cell
NC, nerve cell
NCP, nerve cell process
PG, prothoracic ganglion
PS, prosternum
PT, pretergum
PTF, posterior transverse cervical fold
PVCS, posterior ventral cervical sclerite
SG, suboesophageal ganglion
TC, trichogen cell
V, vacuole in trichogen cell
VCN, ventral cervical nerve.
S, seta



FIGS. 1–6—(1–4) Diagrams of the left side of the neck to show the sclerital areas bearing tactile setae (*solid black*), sclerital areas free from sensory setae (*white*) and arthrodial membrane (*dotted*) in : (1) *Locusta migratoria* L. ; (2) *Gryllulus domesticus* L. ; (3) *Periplaneta americana* L. ; (4) *Forficula auricularia* L. (5) High power view of a tactile seta on the edge of the anterior transverse fold of the neck of *F. auricularia* (× 500). (6) Diagrammatic section of the neck, viewed from the left, to show the cervical nerve supply to tactile setae on the right.

Setal Nerve Supply (fig. 6)

The groups of sensory setae in the earwig neck are all innervated from the prothoracic ganglion (*PG*). A lateral nerve (*LN*) arises postero-laterally from the suboesophageal ganglion (*SG*) and runs backwards, lateral to the double ventral nerve cord, to enter the prothoracic ganglion antero-laterally. On each side, a ventral cervical nerve (*VCN*) from the setae of the ventral cervical sclerites and prosternum runs backwards and enters the lateral nerve (*LN*) just behind the cephalic neck muscles. Before this junction there enters a lateral cervical nerve (*LCN*) from the anterior cervical fold and latero-ventral neck sclerite, running backwards, mesad to the neck muscles. At the same junction a latero-dorsal nerve (*LDN*) from the setae on the latero-dorsal sclerites, pretergum and pronotum enters the ventral neck nerve. Sensory setae on the gular sclerite and the posterior surface of the cardines are innervated by lateral nerves from the suboesophageal ganglion.

Functions of the Cervical Sensory Setae

When the head is rotated in a sagittal plane, the setae on the latero-dorsal sclerites, the pretergum and the anterior cervical fold are rubbed against the rear of the head. The vertical row of setae on the anterior cervical folds are so arranged that, as the head is lowered, the dorsal setae are first stimulated and then those in a more ventral position. Lateral head movements are perceived mainly by the setae on the latero-ventral sclerites and latero-dorsal sclerites. Movements of arthrodial membrane under the anterior margins of the central cervical sclerites and prosternum are perceived by the sensory setae of these sclerites. The setae on the gular sclerite and cardoes are rubbed against the neck during feeding, when the neck is partially retracted. Thus these setae, mentioned above, enable the insect to perceive the position of the head relative to the thorax, that is, changes in the position and form of the neck, as well as the positions of the maxillae and labium.

Discussion

The feeding habits of *Locusta* are associated with head movements in the sagittal plane, which occur mainly at the occipital condyles (*CON*). The setae on the anterior lateral cervical sclerites occur close to the condyles and rub against the postgenae as the head is moved up and down. If these tactile setae are to function efficiently as proprioceptive organs, it is essential they should be attached to a firm base, the rigidity of which is not affected by head movements, and that the hair plates should not be covered by arthrodial membrane. The first condition is fulfilled by the lateral neck sclerites and the second by the arthrodial membrane being gathered at four points on the rear of the head, one pair just above the condyles and the other pair just below them, thus leaving a triangular region of permanently tight arthrodial membrane round each hair plate. The pair of lateral hair plates and setae on the pronotal margin are so placed as to be affected by dorsoventral as well as the small lateral head movements (fig. 1). In the cricket (fig. 2), the head can be moved from side to side as well as in the sagittal plane and rotated about the longitudinal body axis. The cricket head is spherical and fits into the front of the prothorax so that a ball-and-socket joint is formed. The cricket neck resembles that of the locust, but lateral head movements are perceived by two pairs of transverse hair plates situated on the latero-ventral and latero-dorsal sclerites (fig. 2, *LVS*, *LDS*). These, with the hair plates on the lateral cervical sclerites, are adequate to perceive head movements in the sagittal and transverse planes. Two rows of small ventral cervical sclerites restrict cervical folding to a few main tracts (indicated by the dotted lines in fig. 2), while tactile setae on these sclerites perceive arthrodial membrane movements.

The neck of the cockroach (fig. 3), in general, resembles that of the cricket, but

with some notable differences. Cockroaches are dorsoventrally flattened, living under bark and litter through which they force their way by means of the dorsal pronotal shield and posteriorly directed legs. The cockroach head is transversely flattened and normally flexed in an opisthognathous position. When feeding, the head is rotated forwards into a hypognathous position and is then capable of a wide range of movement, similar to that of the cricket. The cockroach neck has two well-developed transverse sclerites that give ventral cervical support, and the greater degree of cervical flexibility is associated with the relatively more posterior position of the setae on the anterior lateral cervical sclerites as compared with the cricket, and with the occurrence of the tactile setae of the pronotum on the ventral side of the shield.

In *Forficula auricularia* there is a similar distribution of tactile setae, but the complexity of the neck and the development of the anterior cervical folds are associated with a greater development of the lateral setae, while those on the pronotum are of little importance. With the reduction in the size of the lateral cervical sclerites, the hair plates have disappeared and their function is now performed by the hair plates situated on the anterior transverse cervical fold. A comparison of the setal distribution in the necks of the four insects is shown in figures 1–4.

It is a debatable point whether or not the absence of ventral cervical sclerites in the locust is a primitive orthopteran feature. In the cricket, these small ventral cervical sclerites form a firm base for the sensory setae and restrict folding of the arthrodial membrane to a few well-defined tracts. In the cockroach and earwig, these sclerites also give ventral cervical support. In the locust and cockroach, the ventral longitudinal cervical muscles originate on the apophysis of the prosternum and are inserted on the tentorial bridge of the head, after mutually crossing in the mid-ventral line. In the earwig these muscles are represented by the anterior ventral longitudinal muscles, which originate on the tentorium and are inserted on the posterior ventral cervical sclerite, and by the posterior ventral longitudinal muscles, which are inserted on the posterior lateral cervical sclerites and originate on the prosternal apophysis. If the form and function of the ventral cervical sclerites of the series *Locusta*, *Gryllulus*, *Periplaneta* and *Forficula* represent stages in the evolution of an intersegmental sclerite in the arthrodial membrane, it would appear that these sclerites first arise to form a base for the proprioceptive setae and/or to restrict folding of the arthrodial membrane to a few well-defined tracts. As these sclerites enlarge, they give increased support and finally form a point of insertion for nearby muscles.

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THE MESOTHORACIC INDIRECT FLIGHT MUSCLES OF SIMULIIDAE AND PSYCHODIDAE (DIPTERA), WITH A NOTE ON THE TERGAL DEPRESSOR OF THE TROCHANTER

By V. J. I. Grant

(*Department of Zoology, University of Bristol*)

The indirect flight muscles of the mesothorax of Simuliidae and Psychodidae differ not only in their number but also to some extent in their structure. In *Simulium ornatum* Meig. (Hinton, 1959*a*), there are on each side of the mesothorax, six dorsal longitudinal muscles, two oblique dorsal muscles, two tergo-meral muscles, two tergo-sternal muscles, and five tergo-pleural muscles (fig. 1). All of these muscles are of the fibrillar type.

In *Psychoda phalaenoides* L., each side of the mesothorax has three dorsal longitudinal muscles, one oblique dorsal muscle, and two tergo-sternal muscles (fig. 2). Thus there are 17 indirect flight muscles on each side of the mesothorax in *Simulium*, whereas there are only 6 in *Psychoda*, but the muscles in *Psychoda* have more fibres. The tergal depressor of the trochanter is present in both families.

In *Pericoma nubila* Meig., the number and arrangement of the indirect flight muscles are the same as in *Psychoda*, except that they are larger in size with more fibres. For instance, the anterior and posterior tergosternal muscles of the mesothorax have 27 and 15 fibres respectively in *Pericoma*, whereas there are 10 and 9 in *Psychoda*. Also, the tergal depressor of the trochanter has 21 fibres in *Pericoma* and 19 in *Psychoda* (fig. 3).

The tergal depressor of the trochanter in *Simulium* is a fibrillar and not a tubular muscle, as has been pointed out by Hinton (1959*b*). In the related family Psychodidae, however, it is of particular interest to note that the tergal depressor of the trochanter is of the tubular type in *Psychoda phalaenoides* L., whereas in *Pericoma nubila* Meig., also a Psychodid, it is of the fibrillar type.

As many writers have noted, the tergal depressor of the trochanter is used as a " starter " muscle : the fly jumps as it begins to fly ; and Smart (1959) points out that all of the long-legged Nematocera which certainly do not jump at the commencement of flight lack this muscle. The presence of a fibrillar " starter " muscle in *Pericoma* and a tubular one in *Psychoda* is unexpected : it would be of interest to know if there are differences in the behaviour of the two flies that can be attributed to differences in the structure of their " starter " muscles.

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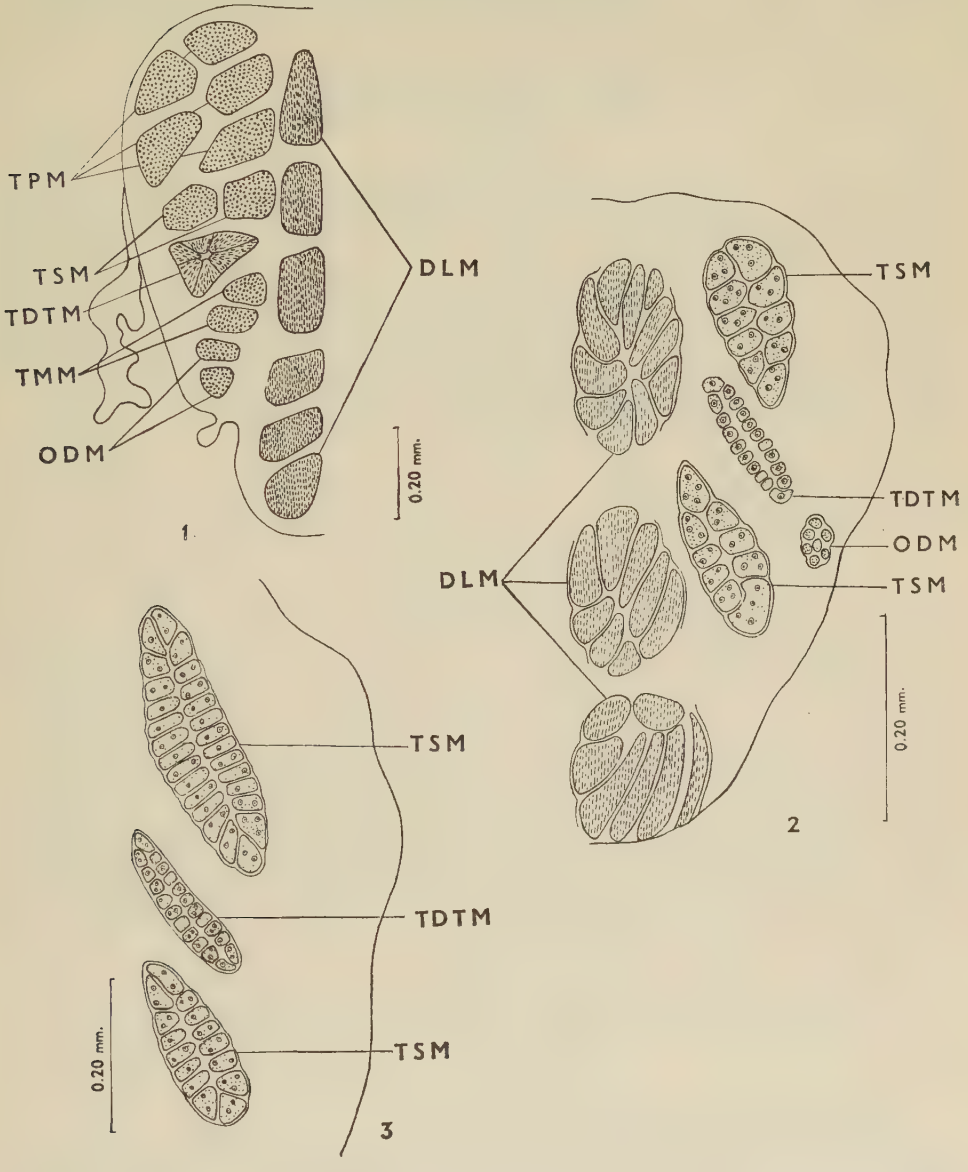

Figs. 1–3.—Horizontal longitudinal sections of the mesothorax showing only the indirect flight muscles and the tergal depressor of the trochanter : (1) *Simulium ornatum* Meig. ; (2) *Psychoda phalaenoides* L. ; (3) *Pericoma nubila* Meig. (Tergal depressor of the trochanter and tergo-sternal muscles only.)

(*DLM*, Dorsal longitudinal muscle ; *ODM*, oblique dorsal muscle ; *TDTM*, tergal depressor of the trochanter muscle ; *TMM*, tergo-meral muscle ; *TPM*, tergo-pleural muscle ; *TSM*, tergo-sternal muscle.)

QUEEN SUBSTANCE PRODUCTION BY VIRGIN QUEEN HONEY-BEES (*APIS MELLIFERA* L.)

By C. G. Butler

(*Rothamsted Experimental Station*)

Introduction

When a mated laying queen honey-bee stops producing enough queen substance, the workers of her colony rear queens preparatory to superseding her or swarming with her (Butler, 1957, 1960).

Virgin queens are not always able to inhibit even small colonies from rearing queens (Butler, 1957), though this is seldom apparent because larvae suitable for rearing as queens are rarely present. The quantities of queen substance extractable from virgin queens have now been measured and found to be less than those extractable from mated laying queens capable of inhibiting queen rearing in large colonies.

Methods

Each of the following queens was extracted in 5 ml. ethanol for 48 hours in a micro-Soxhlet apparatus:

(*a*) Four virgin queens each 24 hours old.

(*b*) Four virgin queens each 7–8 days old.

(*c*) Four virgin queens each 21 days old.

(*d*) Six mated laying queens from normal colonies in which queens were not being reared.

(*e*) Three virgin queens, each 21 days old, which were laying eggs.

The solution from each queen was diluted with an equal amount of ethanol (to make a $\frac{1}{4}$ S. dilution) and assayed in the way described by Butler (1960).

The queens of group (*e*) had been anaesthetised with carbon dioxide for five minutes when seven days old and again when nine days old, with the result that each was laying well when three weeks old (*see* Mackensen, 1947). These queens were included because it seemed possible that the amount of queen substance produced by a virgin (or mated) queen may depend on the state of activity of her ovaries.

A combined extract of 136 mated laying queens from colonies in which queens were not being reared was assayed at various dilutions to provide a scale with which to compare the abilities of the different categories of virgin queens to inhibit queen rearing.

Results and Conclusions

The results (Table I) indicate that little or no queen substance was present in the extracts from virgin queens 24 hours old; week-old virgins had significantly more ($P < 0{\cdot}01$), and virgins three weeks old, whether laying or not, had much more ($P < 0{\cdot}001$). Nevertheless, virgins three weeks old which were not laying eggs had significantly less queen substance than mated laying queens ($P < 0{\cdot}01$), and even laying virgins three weeks old apparently had less ($P < 0{\cdot}05$).

A comparison of these results with those using different dilutions of the standard combined extract of 136 mated laying queens (Table I) suggests that newly emerged queens have little or no queen substance and a week-old virgin has about one-fourth the amount of a normal mated laying queen—*i.e.* about the same quantity as a superseded queen or a swarm queen from an uncrowded colony (Butler, 1960); whereas a three-week-old virgin queen, if not laying eggs, produces about one-third as much, and slightly more when laying.

TABLE I.—*Mean number of cages of bees in which queen cells were produced after supplying various dilutions of extracts of different types of queen* (12 *cages per observation ; standard errors in brackets ; dilution* 1 *S. = extract of* 1 *queen in* 2·5 *ml. ethanol*)

Source of extract	Number of observations	Concentration of extract				
		1/4 S.	1/8 S.	1/16 S.	1/32 S.	*Nil*
Single virgin queens, 24 hours old	4	11·50 (0·29)	.	.	.	12·00 (0·00)
Single virgin queens, 7–8 days old	4	6·75 (0·75)	.	.	.	11·00 (0·00)
Single virgin queens 21 days old (not laying eggs)	4	4·25 (1·03)	.	.	.	12·00 (0·00)
Single virgin queens 21 days old (laying eggs)	3	2·70 (1·45)	.	.	.	10·70 (0·67)
Single mated laying queens .	6	0·33 (0·21)	.	.	.	11·17 (0·31)
		(7 tests)	(6 tests)	(4 tests)	(5 tests)	(7 tests)
Pooled extract of 136 mated laying queens .		0·57 (0·20)	1·33 (0·33)	7·75 (0·48)	10·00 (0·71)	11·71 (0·18)

These results explain the inability of virgin queens always to inhibit even small colonies of bees from rearing queens.

Four and a half hours or longer after removal of a queen from a colony, when the amount of queen substance among the worker bees has become attenuated, it is more difficult to replace a mated laying queen by another than immediately after removal of the queen (Butler and Simpson, 1956). Therefore, the difficulties often experienced when attempting to substitute a mated laying queen for a virgin queen could be explained by the small amount of queen substance produced by the virgin.

It is clear, however, that colonies do not distinguish between queens (*i.e.* virgin, mated, *etc.*) by the relative amounts of queen substance on their bodies, because a young virgin queen with little or no queen substance is better received than an old virgin queen with a moderate amount as a replacement for a mated laying queen with abundant queen substance (Butler and Simpson, 1956). There must, therefore, be an additional factor by which virgin queens are distinguished from laying queens.

SUMMARY

(1) The quantities of queen substance obtainable from virgin queens increased with age and was greater when they were laying than when they were not and was always less than that from mated laying queens.

(2) The inability of a virgin queen to inhibit queen rearing, and the difficulty of replacing a virgin queen by a mated laying queen are probably both explicable by the small amount of queen substance in colonies headed by virgin queens.

(3) Some factor other than queen substance output enables colonies to distinguish between different types of queens.

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1961

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